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by

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New Species in the *Drosophila ananassae* Subgroup from Northern Australia, New Guinea and the South Pacific (Diptera: Drosophilidae), with Historical Overview

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ABSTRACT. Three new *Drosophila* species are described in the *ananassae* subgroup from Australia, New Guinea and Samoa. *Drosophila pandora* sp.nov. and *D. anomalata* sp.nov. are morphologically very similar to the circumtropical species *D. ananassae* and are classified together in the *ananassae* complex. For 40 years *D. pandora* has been incorrectly identified as *D. ananassae* in the Australian tropics. The results of a detailed examination of the morphology of 1649 wild-caught *ananassae*-like male specimens, sampled from 60 islands from Southeast Asia to French Polynesia and 94 localities of northern Australia and western, central and eastern New Guinea, are reported. Comparisons are made with Afrotropical and Oriental samples to confirm the identity of *D. ananassae* s.str. Photomicrographs of the male terminalia and sex combs of *D. ananassae* and *D. pandora* from geographically distant localities demonstrate the stability of the important diagnostic characters. Males of *D. anomalata*, known only from three localities in Queensland, Australia, have a unique bobbing behaviour when courting, and they have the lowest total number of teeth in the sex combs. The distinctive male terminalia of related species *D. atripex*, *D. monieri*, *D. ochrogaster*, *D. parapallidosa* and *D. pallidosa* are figured for comparison. Among them, a species from Samoa, closely resembling the Fijian endemic species *D. phaeopleura*, is described here as *Drosophila schugi* sp.nov.

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Bock & Wheeler (1972) revised the *Drosophila melanogaster* species group (Sturtevant, 1942) worldwide and classified 64 species into 11 subgroups, one of which—the *D. ananassae* subgroup (Hsu, 1949)—was subdivided into the *biplectinata* complex (in males of which the aedeagus is bifid and bare), and the *ananassae* complex (in males of which the aedeagus is fused and strongly hirsute) (Bock, 1971). Two additional

complexes have been added for species from Madagascar and the Seychelles. There are now 336 species in the *melanogaster* species group, they are in 27 subgroups, 25 species are in the *ananassae* subgroup; 15 of the 25 species have not formally been placed in any species complex.

Fieldwork since 1972 in New Guinea, northern Australia and the South Pacific has yielded an enormous cache

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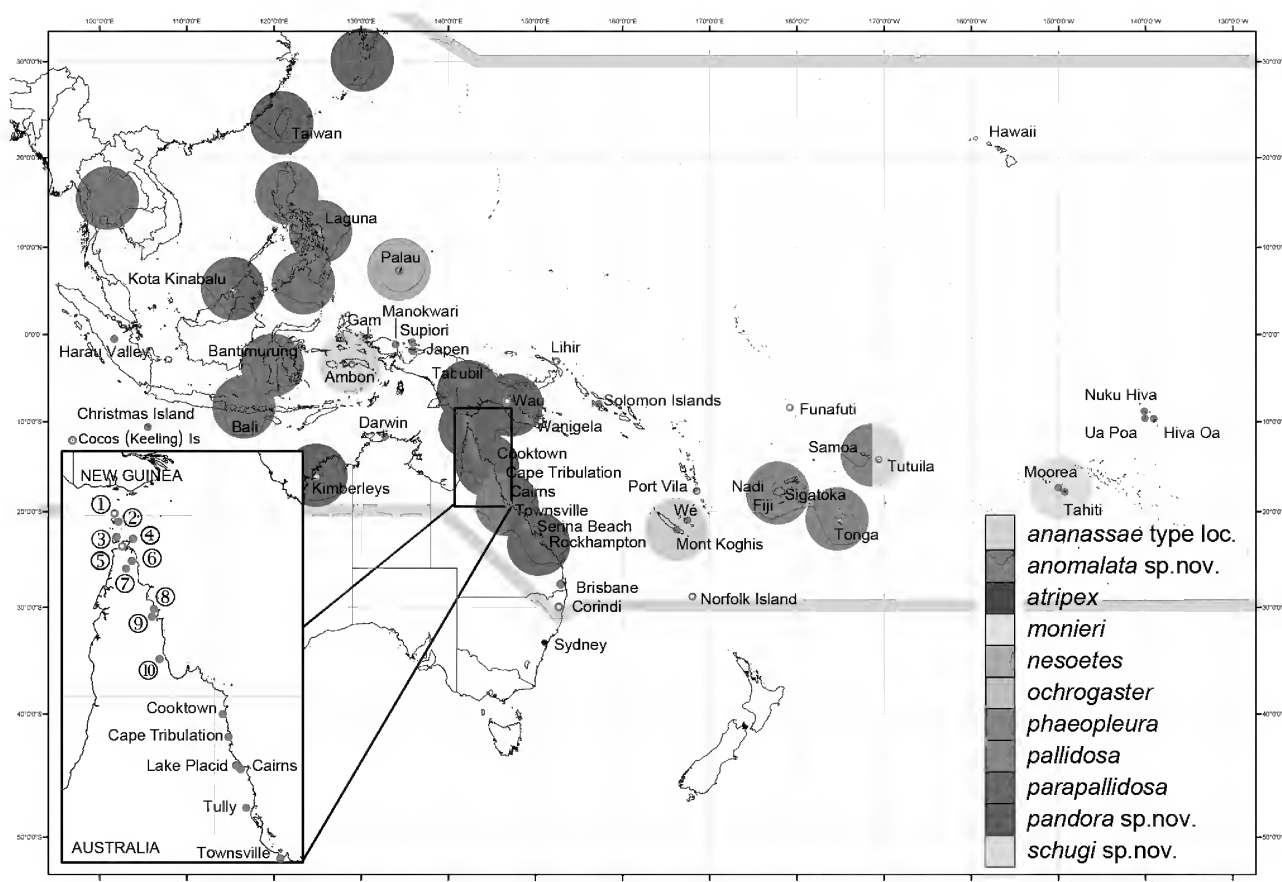


Figure 1. Distribution of 11 of the 12 *Drosophila ananassae* complex species, the authors have collected at red dot localities or examined specimens collected by others from red circle localities; these data are complete for the Australian Region and incomplete for the Oriental Region. *Drosophila lachaisei* Tsacas, 1984 from Africa is not shown. The *Drosophila pandora* sp.nov. type locality is Lake Placid near Cairns (see inset); the *D. anomalata* sp.nov. type locality is Deeragun near Townsville. *Drosophila ananassae* s.str. is pantropical within the pale blue lines, the Ambon type locality is shown; *D. ananassae* extends as far south as Corindi in Australia, it is absent in Sydney and New Zealand. Three or more additional, but undescribed species, occur in New Guinea (and perhaps also in northern Australia), these are not shown. Islands of Torres Strait: (1) Mabuiag, (2) Moa, (3) Thursday, and (4) Mount Adolphus; and localities on Cape York Peninsula: (5) Bamaga, (6) Bertie Creek and Heathlands homestead, (7) Doublemouth and Gunshot Creeks, (8) Gordon Creek, (9) Iron Range (nr airstrip), and (10) upper Peach Creek (McIlwraith Range) are indicated (see inset). Geospatial coordinates of all localities are given in Appendix 1.

of specimens which has enabled us to undertake a comprehensive comparative morphological study of the species similar to *Drosophila ananassae* in this region. In this paper we describe three new species in the *ananassae* subgroup, two of which are in the *ananassae* complex.

Historical overview

To introduce the discovery of these cryptic species, it is necessary to provide historical, biogeographic, genetic and taxonomic context that is more expansive than usual. *Drosophila pandora* has been confused, especially in Australia, with the cosmopolitan species *Drosophila ananassae*—an extremely important model species used in hundreds of labs worldwide. The possibility that anomalous experimental outcomes are attributable to there being more than one species under study, is worth exploring.

Quite apart from the availability of a range of formal and informal potential synonyms, there is also a very long history of intensive population, genetic and evolutionary study of

very similar species collected within and near the known range of the new species. Teams of biologists, primarily in Japan, the United States and Australia, have, for many decades, used live strains of “*Drosophila ananassae*”—established from flies collected from the New Guinea region and islands of the South Pacific—to explore various important questions in evolutionary biology. Unfortunately, many of the significant cytological, karyological, and behavioural discoveries have been published using informal strain-names and codes and their utility over the decades has been found wanting because reliable voucher specimens are now difficult to find or are lost. In the following discussion, advances in taxonomy are introduced in approximate chronological order to help explain how certain assumptions have, in some ways, inhibited overall progress. The authority of a school of thought or a single major publication often has strongly influenced the direction of enquiry. At the end of this work we conclude that the centre of diversity for the *ananassae* complex is New Guinea. New Guinea and the northern part of Cape York Peninsula, is a tropical region

that has had continuous, land-connected, lowland rainforest for most of the last two hundred thousand years (Williams, 2001).

Carl Ludwig Doleschall (1859) discovered and named *Drosophila ananassae* at Ambon, just to the west of New Guinea where he was based as a young doctor and entomologist (Fig. 1, Indonesia). At the time he read the publications describing insects that were being collected by his contemporary—Alfred Russell Wallace—further to the west in the *Dutch East Indies* (= modern Indonesia). Wallace sent his specimens back to London where Walker described them. Doleschall stayed abreast of Wallace's discoveries because copies of Walker's publications were being sent to him by Bleeker. Soon after receiving two works (*Journal of the Proceedings of the Linnean Society* 1856) enumerating new dipterous species Wallace had collected in Singapore, Malacca, Sarawak and Borneo, Doleschall and Wallace actually met at Ambon in December 1857. Five months later, in May 1858, Doleschall collected specimens in Ambon that were subsequently to become the types of his new species *Drosophila ananassae* Doleschall, 1859. He described their abundance as *Zeer talrijk op saprijke zoete vruchten in bederf beginnen te overgaan; vooral op de rijpe vruchten van ananas* [numerous on sappy and sweet fruit which has become overripe; especially on ripe pineapple]. Having carefully read Wallace's Linnean Society publications, and possibly encouraged by Wallace several months earlier, Doleschall convinced himself that the species had not already been described from Wallace's collections on islands to the west. His manuscript, although submitted and dated 1858, was actually published in April 1859. Just two months earlier, in February 1859, Doleschall died. To the best of our knowledge no-one has re-collected *Drosophila* species at the Ambon type locality and the Doleschall's type specimens are apparently lost (Brake & Bächli, 2008). Evenhuis & Greathead (1999) note that a portion of the Doleschall deposition in the Naturhistorisches Museum Wien was shipped to the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMHB), on 15 April 1860; but Bächli (1984) examined the Drosophilidae in the ZMHB and found only one taxonomically important specimen of *D. ananassae*—a paratype male of *D. caribea* Sturtevant, 1916 (= *D. ananassae*), from Havana, Cuba, collected 1915. In the present study we have collected at various localities surrounding Ambon: at Bantimurung, Manokwari, Supiori, Japen and Darwin (Fig. 1) and we have examined *D. ananassae* from Gam Island (Fig. 1, sample provided by Andrew Davis) but unfortunately still not from Ambon.

Hundreds, if not thousands, of other papers on the genetics, cytology, and reproductive biology of *Drosophila ananassae* have followed (Tobari, 1993). A search of *Drosophila ananassae* using *Google Scholar* reports approximately 175,000 results. It is a species of considerable genomic importance (Stark *et al.*, 2007).

Interest in the genetics and cytology of *D. ananassae* began as early as 1921 (Sturtevant, 1921), some 60 years after Doleschall's publication. Sturtevant (1916) was based in North America, and had inadvertently overlooked Doleschall's (1859) original description and renamed the species *D. caribea* from specimens collected in Cuba. Sturtevant did not know at the time that the species was pantropical. Kikkawa (1935) in Japan, on receiving a strain of *D. caribea* from Sturtevant, established its synonymy

with local *D. ananassae* (Moriwaki, 1993). From the 1930s onwards, various Japanese and North American researchers and their students made *D. ananassae* the principal model for genetic investigation—the species, as a living culture, was easily sustained in labs. Moriwaki began working with *Drosophila ananassae* mutant strains in Japan in 1931. Kaufmann studied *D. ananassae* cytology at the University of Alabama, publishing results in 1936–1937. Moriwaki collaborated with Kikkawa in Komai's lab at Kyoto and by 1938 Kikkawa and Moriwaki had discovered over 100 mutations of *D. ananassae*, and spontaneous crossing over in males. Despite dispersing four replicates of their large and valuable collection of mutant stocks prior to WWII, none survived. From 1948, collaboration with Dobzhansky and Patterson resulted in renewed investigation of *D. ananassae* in Japan and in the United States (Moriwaki, 1993). Notwithstanding the significant growth in the use of various other *Drosophila* species worldwide as model organisms in genetics, it is the evidence of *population structure* in *D. ananassae* (cf. *D. melanogaster*) that elevates its status as an ideal model for the study of natural selection on genomic variation (Schug *et al.*, 2007).

“Among the relatively small number of species in the genus *Drosophila* that have been subjected to cytogenetic analysis, *D. ananassae* is unique in having appreciable levels of meiotic crossing over in males (Kikkawa, 1938; Moriwaki, 1940; Hinton, 1970; Moriwaki *et al.*, 1970). Still other unusual features attributed to this species include remarkably varied chromosomal polymorphisms (Dobzhansky & Dreyfus, 1943; Freire-Maia, 1961; Futch, 1966), high mutability (Kikkawa, 1938), Y-4 linkage of the nucleolus organizer (Kaufmann, 1937), segregation distortion (Mukherjee & Das, 1971), parthenogenesis (Futch, 1972), and extrachromosomal inheritance (Hinton, 1974)” (Hinton & Downs, 1975:353). “Almost the entire *Wolbachia* genome has been transferred into the second chromosome of *D. ananassae*. Following this lateral gene transfer, *D. ananassae* transposable elements have become inserted within *Wolbachia* genes. At least 28 *Wolbachia* genes are transcribed from within the *D. ananassae* genome, although the functional significance of this is unknown” (Werren *et al.*, 2008). Evidence of precopulatory sexual selection has been demonstrated in *D. ananassae* by using laser surgery to manipulate trait size—Grieshop & Polak (2012) show that incremental reductions of spine length progressively reduce male copulation success.

Drosophila ananassae is a peridomestic species in every tropical region of the world (Patterson & Mainland, 1944; Gupta & Ray-Chaudhuri, 1970; Buruga & Olembo, 1971; Lachaise, 1974; Brncic, 1987; Tobari, 1993; Brake & Bächli, 2008): Oriental, Australian (including all of the island groups of the Pacific), Afrotropical, and Neotropical. The species has even been reported from the Palaearctic and Nearctic Regions (David & Tsacas, 1981). But it is important to note that cryptic species do exist sympatrically in many localities (Fig. 1 and Schug *et al.*, 2007) and quite often *D. ananassae* s.str. is, in fact, rare or absent. Among 56 species (14 genera) collected in urban Kuala Lumpur, Malaysia, Takada & Momma (1975) found not a single specimen. At Lake Placid near Cairns (Fig. 1) the relative abundance of *D. ananassae* at fruit bait changes throughout the year and over short distances (see Discussion).

Drosophila ananassae appears to be the most common

drosophilid species on islands scattered across the Pacific (Wheeler & Takada, 1964). Bezzi (1928) recorded it from Fiji. Malloch (1934a,b) reported *D. errans* (a replacement name for *D. similis* Lamb which was later recognized as a synonym of *D. ananassae*) from the Marquesas islands and from Samoa (Apia and Malololelei on Upolu and Salailua on Savaii, also American Samoa). Curran (1936) reported *D. ananassae* from Anuda and Puka Puka, Cook Is, and Matema Island, Santa Cruz Group. Pipkin (1952, 1953) studied the population fluctuations of four *Drosophila* species, including *D. ananassae*, on Moen Island (Truk, Caroline Is). Harrison (1954) reported *D. ananassae* from Western Samoa (Vailima [low hills behind Apia] and Malololelei, Upolu). Mather (1955, 1960) reported “*D. ananassae*” from urban and rainforest localities (Tolga, Tully, Babinda, Thursday I, Crystal Cascades, Redlynch, Cairns and Lake Barrine) in northern Queensland, Australia.

Mather’s Australian determinations are uncertain and were ignored by Bock & Wheeler (1972) when they summarized *D. ananassae* distributional information. They were overlooked probably because, a year earlier, Bock (1971) had established that Mather’s concept of “*D. ananassae*” included *D. pseudoananassae* Bock, 1971. Also, Mather (1955: 570) described the sex combs as *Transverse ... on first leg; two on 1st tarsal segment and one on 2nd tarsal segment*, this arrangement is quite unlike *D. ananassae* (see Figs. 60–65) and very similar to *D. pseudoananassae*. There is circumstantial evidence that Mather inadvertently lumped together several species under the label “Australian *D. ananassae*”. One iso-♀ stock supplied to Texas by Mather was used later by Spieth (1966) who found it (Texas 2372.11) to be neither *ananassae* nor *pseudoananassae* (see below) (see also Kaneshiro & Wheeler, 1970). In the present study we have collected *D. ironensis*, *D. bipectinata* Duda, 1923, *D. pseudoananassae*, *D. ananassae*, *D. pandora* and *D. anomalata* (see below) in the Tully–Babinda–Cairns–Thursday Island region where Mather only reported the one species—“*D. ananassae*”. This early history and confusion is important to understand because it will be shown that these species of the *ananassae* subgroup are among the most abundant drosophilids at fruit baits throughout the Wet Tropics of Australia (see Discussion), yet right up until the mid-1970s there was nothing in the literature (except Mather’s questionable data under the name “*D. ananassae*”) that indicated this.

After 1957 the recognition of *D. ananassae* as a species of considerable value among the many available in the study of genetics, cytology and evolution grew rapidly. New strains were collected and added to the growing bank of cultures in Japan and the US (at the University of Texas). In 1955 and 1956 Stone *et al.* (1957) studied *D. ananassae* from the Marshall Islands and the eastern Caroline Islands. Their results provided estimates of the degree to which direct and fall-out radiation from “atomic” and thermonuclear tests near Bikini in 1954 and 1956 impacted on natural populations. Wild caught flies from all over the Pacific were shipped back to labs at Texas where they remained in culture and were used, for many years, even decades, in various other studies (Moriwaki, 1993). Numerous additional “*ananassae*” cultures were established from flies collected throughout the Australian and Oriental Regions. Strains from, for example, Fiji, Samoa [then Western Samoa] and nearby American Samoa, Tonga, Nieu, Palmyra, Philippines, Thailand and

several Papua New Guinean localities (Brown River, Popondetta, Bulolo, etc.), had become available for study during the early 1960s. Only one strain appears to have been available from the Australian mainland. Spieth (1966) refers to a “very light yellow” strain of “*Drosophila ananassae*” from northern Queensland and New Guinea (Texas 2372.11) that has a sexual behaviour and a copulation-duration time that he described as distinct among many strains from throughout the Pacific. This, and 16 other drosophilid stocks, were supplied to the Texas Stock Center by Mather in the late 1950s or early 1960s—they all have the 2372 prefix and they correspond exactly to the 17 species he had reported on in his 1955 publication. Texas 2372.11 was determined by Mather to be “*D. ananassae*” (Mather, 1955). We have not been able to obtain voucher specimens of Texas 2372.11. This could have been any one of the following six cryptic species that we have now collected in northern Queensland:

Drosophila ananassae Doleschall, 1859:128
Drosophila anomalata sp. nov.
Drosophila bipectinata Duda, 1923:52
Drosophila ironensis Bock & Parsons, 1978:102
Drosophila pseudoananassae Bock, 1971:274
Drosophila pandora sp. nov.

It has been noted in previous studies that among all strains from throughout the Australian Region (including islands of the Pacific) pigmentation varied—terms such as “dark (black)” “dark (grey)”, “light (grey)” “light (yellow)” and “very light (yellow)” were given to the different “*ananassae*” strains. This was at a time when workers were beginning to suspect that more than one species might be present. Varying degrees of intersterility and courtship behaviour were discovered among certain of these strains (Futch, 1966; Spieth, 1966).

Using the geographic array of strains that were established by the University of Texas Genetics Foundation from across the region, Futch (1966) commenced an investigation of the relationships between cytology (polytene chromosome banding patterns) and intersterility. Working concurrently, Spieth (1966) began a detailed analysis of courtship and mating behaviour. Futch, unlike Spieth, included no Australian strains in his work. Both Futch and Spieth concluded, although Futch more decisively, that cryptic species close to *D. ananassae* existed in New Guinea. “Futch [1966] further demonstrated a high sexual isolation between the New Guinea strains which he used in his investigation and the Pacific dark strain, suggesting that the New Guinea populations represented a separate species. The evolutionary position within *ananassae* is certainly complex; varying degrees of sexual isolation exist between the various populations of New Guinea and the neighbouring British Solomon Islands [an unpublished Bock observation, cited in Bock & Wheeler, 1972]. ... We do not believe that a new species should be recognized among the New Guinea populations of *ananassae* unless further work [is] done to clarify the relative evolutionary status of the various populations in this area, and the relationships of these populations to others of *ananassae* indicates that this is clearly warranted” (Bock & Wheeler, 1972).

Futch (1966) considered the light and dark forms in Samoa to represent separate races from the more widespread cosmopolitan race, *D. ananassae* s.str. “A division of the species into races is proposed partly on the basis of the

geographic distribution of these pigmentation types. The very light forms of the islands of Micronesia and the very dark forms of Polynesia constitute two of these races. The third race is composed of populations of *ananassae* from all parts of the heavily populated tropical and sub-tropical world.” But later Futch (1973) writes: “Flies from the dark populations are definitely *D. ananassae*. The connection between the Samoan dark *D. ananassae* [insular population] and the body [widespread panmictic population] of the species is demonstrated by the discovery of two of the three inversions found in many other populations of *D. ananassae*, particularly those living in areas of large and active human habitation.” Further, he writes “Electrophoretic analysis of each of the five samples [of *D. pallidosa* Bock & Wheeler, 1972, and *D. ananassae*, collected during the Samoa 1965 Expedition] showed that the two species differ significantly and consistently in Samoa in the relative frequencies of a certain set of esterase alleles, i.e., Esterase-C (Johnson *et al.*, 1966a). ... In addition, the Papuan [then equivalent to eastern not western New Guinea] forms apparently represent a third species which has yet to be named.” The suggestion is made that these three species [*D. ananassae*, *D. pallidosa* and an unnamed taxon from New Guinea] may represent a part of a complex of *ananassae*-like species which have evolved in the Australia–New Guinea area. Futch suggested in a pers. comm. to Tobari (Tomimura *et al.*, 1993: 147) that the name “papuensis” [sic] could be used should this unnamed taxon be described as a new species. This name has, however, never been proposed formally and “papuensis” remains a nomen nudum; it should not be printed in italics as if it were a formal species name.

The taxonomists, Bock and Wheeler, while they worked together at the University of Texas (1970–1972), described *D. pallidosa* and *D. phaeopleura* Bock & Wheeler, 1972 from some of the above established strains. Texas strain 3044.12 collected in Fiji in 1966 by Wheeler and referred to as the “light” form of “*ananassae*” was named *D. pallidosa*. Texas strain 3044.4, also collected in 1966, and tentatively referred to as “sp. 5” with pigmentation a “bit darker” (Kaneshiro & Wheeler, 1970) and “brown (darkening considerably with age to dusky)” (Bock & Wheeler, 1972) became the new species *D. phaeopleura*. Importantly, the two experienced taxonomists, emphasized the remarkable morphological similarity of *D. pallidosa* and *D. ananassae*: “exceedingly similar species” that “cannot be separated by detailed examination of the male genitalia”.

What is the relationship between the strains described as “light (yellow)” (Texas strains 3020.8 and 3021.2), “very light (yellow)” (Texas strains 3020.9 and 3021.3) originating from Papua New Guinea, and true *D. pallidosa* from Fiji? Are these all *D. pallidosa*? Or is the light versus dark differentia unreliable away from the Fijian type locality? These questions were unanswered by Bock & Wheeler (1972) and for 40 years uncertainty has surrounded the *ananassae*-complex at its probable biogeographic centre: in and around New Guinea—a region that incidentally includes the type locality of *D. ananassae* at Ambon (Fig. 1) and two of the three species described as new in the present study. All flies we have collected and determined to be members of the *ananassae* complex from northern Australia–New Guinea are pale. Among all the Australian (in the geopolitical sense) samples, Bock (Bock, 1986:306) found that only *D. ananassae* from the very isolated Norfolk Island

(Fig. 1) were very dark having the “Fijian coloration”. We have examined these specimens (ANIC 29031439–451) and agree—they are much darker, almost blackish, compared to the individuals of *D. ananassae* we have collected in northern Queensland and New Guinea, the latter are all pale. To the experienced eye the most pallid specimens in Australia and New Guinea are, *D. bipectinata*, *D. ironensis* Bock & Parsons, 1978, *D. pseudoananassae*, *D. pandora*, and *D. anomalata* while mature *D. ananassae* are slightly darker.

Of all the “*D. ananassae*” strains once held at Texas, only 3044.12 and 3044.4 were formally determined to species, the rest were treated as polymorphic “*D. ananassae*”. Nowhere in the literature, as far as we can find, is there a table of disambiguation that authoritatively and clearly links the various descriptors “light” or “dark” etc. to the many “*ananassae*” strains of variable pigmentation originating from islands of the Pacific. Very soon after 1972 the light–dark nomenclature was found to be unhelpful and was abandoned. The type cultures of *D. pallidosa*, *D. phaeopleura* have expired but pinned and alcohol-preserved specimens continue to be available in some cases.

A further challenge in taxonomy is that most previous research derives from populations sourced at locations far from the probable biogeographic centre of the *ananassae* complex. The type specimen of *Drosophila ananassae* is lost (Rocha Pité & Tsacas, 1980; Bächli, 1982; Brake & Bächli, 2008). No cultures of *D. ananassae* from the type locality in Ambon (Indonesia) have ever been established, indeed no reference is made, anywhere in the literature, to specimens collected from there since 1858. Some of the world’s most inaccessible terrain—rainforests of New Guinea and nearby islands to the west in Wallacea and to the east in Melanesia, and “islands” of rainforest stretching 800 km to the south along the largely uninhabited eastern side of Cape York Peninsula, Australia—seriously curtail systematic sampling at the centre of the complex. Until the present study, most species of the *ananassae* complex are reported from localities to the west, northwest, east and south of New Guinea but not New Guinea itself (Fig. 1) (but see Tobari, 1993).

When Bock & Wheeler (1972) described new *ananassae* group species from across the Pacific, from Malaysia to Samoa, why did they not encounter the new species *D. pandora* and *D. anomalata* proposed here, which we have found to be common on Cape York Peninsula, at Darwin (Fig. 1) and at certain localities in New Guinea? What evidence did Bock & Wheeler (1972) present that *D. pallidosa* is an insular island-endemic with a distribution limited to Fiji and Samoa? Are the specimens that are currently catalogued as *D. pallidosa* at the San Diego Stock Centre actually derived from the type culture and, if not, how was it established that they are actually conspecific with *D. pallidosa*? Are specimens of Futch’s (1966) original Papua New Guinea stocks available for study? When Bock (1976) revised the Australian species of *Drosophila*, only two species of the *ananassae* subgroup were listed, we now know of five. Perhaps an explanation lies in the dearth of material in museum collections at that time. *Drosophila ananassae* was treated as rare “collected in Rockhampton, by J. S. F. Barker, and in Cairns by author [Bock], otherwise apparently unknown from the Australian mainland”, and *D. pseudoananassae* had been collected in a few rainforest localities near Cairns. *Drosophila bipectinata* was not then known from Australia, *D. ironensis* was not discovered,

nothing had been available for study from Darwin (Bock, 1976), and our collections from Iron Range and Torres Strait were the first from Cape York Peninsula (McEvey, 1982; McEvey & Bock, 1982).

In 1981 Y. Fuyama, E. Takanashi, and Y.N. Tobari (Tomimura *et al.*, 1993) collected *Drosophila ananassae* and *D. pallidosa* from Lautoka, Fiji (NAN); Togatapu, Tonga (TBU); Vava'u, Tonga (VAV); and Pago Pago, American Samoa (PPG). They established 60 strains of *D. pallidosa*, 40 strains of *D. ananassae* and 101 strains of “dark” *D. ananassae* from these localities (Tomimura *et al.*, 1993: table 1). They also collected 10 strains of *D. ananassae* and two of “*D. pallidosa*” from Noumea (NOU), New Caledonia. The report of “*D. pallidosa*” from Noumea should probably be corrected to *D. ochrogaster* Chassagnard, 1992; *D. ochrogaster* was described in a work published almost simultaneously. These strains, and additional ones from New Guinea, have been given four informal names: “*pallidosa*-like” (Tobari, 1993:147); “*pallidosa*-like Wau” (Matsuda *et al.*, 2009:159); “papuensis”; and “papuensis-like” (Tobari, 1993:147). The name “papuensis” is a suggested name offered by Futch pers. comm. to Tobari [Tobari, 1993:147], as mentioned above, it has never been formally published as a new species’ name and is therefore a nomen nudum, it could be written and treated as a vernacular name. The name “papuensis-like” is synonymized in the present work, see below.

Knowledge of the Drosophilidae of Cape York Peninsula (see inset, Fig. 1) was limited to just a handful of species prior to 1975, none had been the subject of detailed taxonomic study. David K. McAlpine mounted an Australian Museum Diptera-collecting expedition to Iron Range in May–June 1966 and again in 1971–72 with D. P. Sands and G. A. Holloway. All material was lodged in the Australian Museum and all Australian Museum Drosophilidae were later examined during Bock’s taxonomic studies at La Trobe University from 1975 to 1989. Despite the rich diversity of species collected from Cape York by McAlpine and others, surprisingly only two drosophilid specimens (AMS K275443–444) are referable to the *ananassae* subgroup. Bock and Parsons collected 3 drosophilid species at Bamaga (McEvey, 1980a) and 12 at Iron Range in 1975 (Fig. 1, inset no. 5, no. 9). *Drosophila ironensis* was discovered at Iron Range on this expedition together with specimens determined as “*Drosophila ananassae*” by Bock. Bock apparently revisited Iron Range in April 1976 (according to label data) but despite a sample of 20 species in 5 genera, the full richness of the fauna was still significantly underestimated (McEvey & Bock, 1982).

The rich diversity of the drosophilid fauna on Cape York Peninsula only became evident in the early 1980s following McEvey’s expeditions to Iron Range, islands of Torres Strait (Mt Adolphus, Thursday, Horn, Prince of Wales, Moa, and Badu) (McEvey, 1980a,b, 1982; McEvey & Bock, 1982) and the Cairns and Atherton Tableland regions (McEvey, 1980a). “*Drosophila ananassae*” (a very high proportion of which are now referred to the new species *D. pandora* described below), was found to be the most common species at all sites surveyed in Torres Strait, but was found to be relatively rare at Iron Range. Don Colless, as part of a 1980 CSIRO expedition to the Cooktown region, added more drosophilid species to the growing checklist, but still, species of the *ananassae*-

complex were in low abundance (Bock, 1984). North of Iron Range, in the region around Heathlands Homestead (Fig. 1), another survey of drosophilids by McEvey in 1992 brought the total number of Cape York Peninsula species to 213 (35 genera) (McEvey, 1993, 1994). The generic-level diversity of Drosophilidae in the Australo-Papuan rainforests is unparalleled anywhere else in the world (McEvey, *The Drosophilidae of New Guinea*, 8th International Dipterological Congress, Potsdam, 2014).

By the mid-1990s a biogeographic picture had formed: “*Drosophila ananassae*” was common on islands of the Pacific and Torres Strait and according to some reports, also in New Guinea, and rare on the Australian mainland. But, for a number of reasons, and due to a wide range of investigations, this biogeographic interpretation has changed considerably.

At the University of Queensland, Rieks van Klinken, together with Gimme Walter, made considerable advances in understanding the ecology and larval hosts of a large number of Australian drosophilids (van Klinken & Walter, 1996, 2001; van Klinken *et al.*, 2002). Rieks van Klinken conducted field surveys in southern Queensland, in northern Queensland (around Cairns), in far northern Queensland (Iron Range) and in the Northern Territory. His focus on frugivorous species and his scoring of thousands of specimens led him to become aware of, and able to identify, cryptic species that did not fit comfortably within the established taxonomy of Bock, a classification followed confidently by us for most of the last three decades. One species in particular was very common on rotting fruit in northern Australia but it did not conform to the description of *Drosophila ananassae* (or the redescrptions cited in Bock & Wheeler, 1972), it appeared to have sex combs less developed than in typical *D. ananassae*, but slightly more developed than in the combless species *D. ironensis*. In the series of works authored by van Klinken or van Klinken & Walter from 1996 the terms “near *ironensis*”, “*ironensis* (nr)” or “nr *ananassae*” were used for this taxon (or these taxa). Results presented below confirm that this taxonomic caution and questioning of the status quo was prescient.

Tom Starmer, Michal Polak, Stuart Barker and Shane McEvey collected extensively off fruit bait in rainforest at Cape Tribulation in January 2003. Starmer and Polak detected variation in the expression of sex combs in males of “*D. ananassae*” det. McEvey—in some larger, slightly darker, and rarer male specimens, the expression of sex combs seemed lavish or hypertrophic, while in other slightly paler, more abundant, smaller males, it seemed relatively diminutive or feeble and to some extent forming fewer rows. This led them to question whether one or more cryptic species remained undetected in the northern Queensland fauna despite three decades of survey work by Bock, Parsons and McEvey. These observations, together with those of van Klinken, represented the second significant questioning of the taxonomic status quo.

Malcolm Schug, Shelly Gray-Smith, Michael Marshall and Shane McEvey established 50 iso-female lines of “*ananassae* (det. McEvey, 2003)” from Thursday Island, from Cairns, from Fiji, and from Samoa (200 lines in total). Among the strains from Thursday Island and Cairns it was noticed that a small proportion of the males were slightly larger, darker and with more lavishly developed sex combs, but at the time of the study the morphological variation

was still considered by McEvey to be intraspecific (Schug *et al.*, 2007). Nevertheless, evidence was mounting that observed variation was not intraspecific. The results of the Schug *et al.* multi locus population genetic analysis presented very strong evidence of population discontinuity or assortative mating that led, in 2008, to McEvey writing of northern Queensland samples: “The flies with a luxuriant expression of sex combs and dark abdomens I classify as *Drosophila ananassae*. The flies with just 3 rows of teeth on the metatarsus I [now] classify as *pallidosa*-like. The flies with more than 3 metatarsal rows but with less than 36 sex comb teeth in total, might be ‘papuensis’ or ‘papuensis-like’ ... I don’t think anyone knows the morphology of Futch’s [1966] flies ... I plan to examine the terminalia [of Torres Strait specimens] and it will be interesting to see if the morphology falls into three or just two classes. This might take some time. But terminalia usually gives better separation.” McEvey (2008) wrote: “In the *Drosophila ananassae* group ... there remains some confusion about the correlation between genotype and phenotype in northern Australia and New Guinea, it is possible that several undescribed species live alongside *D. ananassae* s.str. in northern Australia, New Guinea and the southwest Pacific.”

During the last four decades a very large collection of *ananassae* complex species has been established at the Australian Museum largely deriving from the various collecting and field surveys outlined above. The opportunity to conduct a wide ranging comparative examination of male terminalia and sex comb morphology of specimens from various parts of New Guinea, from numerous widely dispersed localities of northern Australia and from New Caledonia, Fiji, Samoa and other large island groups of the South Pacific and Oriental Region, has enabled us to conclude that indeed there are consistent morphological characters that allow differentiation of at least two undescribed species close to *D. ananassae* in northern Australia. We formally describe the two new species below.

Such focused and fine-scaled biological scrutiny of living material from hundreds of laboratory strains and isolates has necessarily led to an informal nomenclature for cultures (summarized below). Each culture often has a particular heritable property—“individual iso-female lines collected in Papua New Guinea can be classified into three groups on the basis of the composition of their chromosomal inversions. An examination of the morphological characters of adult flies classified into these three groups (populations) demonstrated that there are some differences in genitalia, sex combs, and spermathecae (Tobari, unpublished).” (Tomimura *et al.*, 1993).

A detailed comparative study of male terminalia and sex comb structure, has been conducted by us using *ananassae*-like samples we have collected (or sourced from others) from wide-ranging localities (Fig. 1 and Appendix). Three new species are described: *Drosophila pandora* sp.nov., *D. anomalata* sp.nov. and *D. schugi* sp.nov. *Drosophila pandora*, is particularly common at fruit bait in tropical Australia, incorrectly identified as *D. ananassae* for several decades, it cultures easily and is likely to become a species of some importance in genetic research. This new species also occurs in New Guinea but we have chosen a strain from Lake Placid near the northern city of Cairns as the type culture, so that future researchers can have easy access to—and more taxonomic confidence about—field samples.

Material and methods

Males have been scored for sex comb configuration and the terminalia of these males has been dissected. In many cases, iso-♀ strains have been established, and males from these strains have been examined. The last two or three segments of male abdomens were removed, soaked in distilled water for 5 minutes, and cleared for c. 8 minutes in hot, almost boiling, 1 molar concentration KOH. Fatty tissue, internal soft organs and abdominal segments were then teased away from the genitalia in a drop of water on a slide using mounted micro-pins (fashioned by forcing a micro-pin, blunt end first, into the sharpened end of a 5 mm diameter wooden dowel, and fixing it with epoxy glue). Further clearing is sometimes necessary at this stage to completely remove soft tissue from the preparation. The terminalia was lifted from the water using a fine-pointed tool and placed in liquid glycerine or glycerine-gel in another welled-slide. The hypandrium and epandrium were then disarticulated using two mounted micro-pins. Specimens can be kept stationary using a small amount of gelatinized glycerine. Photo micrographs were prepared using a Leica M205A microscope with Leica DFC 500 and lit using high diffuse dome illumination Leica LED5000 HDI. Image stacks were processed using Leica Application Suite version 3.8 montaging software (LASv3.8).

Museum abbreviations are as follows:

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANIC	Australian National Insect Collection, Canberra
IRD	Institut de Recherche pour le Développement, Nouvelle Calédonie, Noumea
KIZ	Kunming Institute of Zoology, Chinese Academy of Science, Kunming
MNHN	Muséum national d’Histoire naturelle, Paris
MSRC	Michele Schiffer Reference Collection, Melbourne
MZB	Museum Zoologicum Bogoriense, Bogor, Indonesia
NSMT	National Science Museum, Tokyo
QMB	Queensland Museum, Brisbane
UQIC	University of Queensland Insect Collection, moved in entirety to QMB in 2011
USNM	United States National Museum, Washington DC
WAM	Western Australian Museum, Perth

Abbreviations, morphometrics and indices are given by McEvey (1990), Zhang & Toda (1992), Chen & Toda (2001) and Bächli *et al.* (2004). Numbering orbital setae (McEvey, 1990) has been confusing, instead the following abbreviations are now used for the three fronto-orbital setae: *p.r.orb*—posterior reclinate, *a.r.orb*—anterior reclinate, and *proc.orb*—proclinate; *prorb* = *proc.orb*/*p.r.orb*, and *rcorb* = *a.r.orb*/*p.r.orb* (Zhang & Toda, 1992). Frontal width *fw*, can be measured through the anterior ocellus *fw(a.oc)* (Zhang & Toda, 1992; Chen & Toda, 2001), between the outer verticals *fw(ov)*, between the inner verticals *fw(iv)*, through the anterior reclinate orbital to the eye margin *fw(a.r.orb)* (McEvey, 1990), or as the distance “between upper eye corners” *fw(vt)* (Bächli *et al.*, 2004). At the lower, anterior end of the frons, frontal width is measured “just above the ptilinal suture” *fw(ptl)*—a square frons would have, for example, *fw(vt)* = *fw(ptl)* = frontal length *fl*, whereas a tapering frons narrower at the anterior or lower end would have *fw(vt)* > *fw(ptl)*. The *frontal tapering ratio* of Bächli *et al.* (2004) is *fw(vt)/fw(ptl)*. An oblong eye has a width shorter than the greatest diameter (*o*), the eye width at right

angles to the line of greatest diameter is *ow*. The *dc.gap* is the transverse distance between the bases of the two anterior dorsocentral setae. The *vt-index* of Bächli *et al.* (2004) is the ratio of *iv/ov*. Wing length can be measured from the axillary area to the wing apex (*L.Ax*) (Bock, 1976; McEvey, 1990); from the humeral crossvein to the apex (*WL*) (Grimaldi, 1987; Zhang & Toda, 1992); or from the basal medial bifurcation to the tip of vein R_{4+5} (*L_v*) (Okada, 1959; Bächli, 1971); *prox.x* (position of the proximal crossvein) is the ratio of the penultimate section of vein L3 and the penultimate section of vein L4 (basal R_{4+5} / MIII, Vilela & Bächli [1990]). Body length has been measured in different ways. It can be either the sum of the head, thorax and abdominal lengths, *BL(McE)* (Bock, 1976; McEvey, 1990); or it can be measured from the anterior to posterior extremities of the body: “straight distance from distal edge of pedicel to tip of abdomen”, *BL(Z&T)* of Zhang & Toda (1992).

Paired bristles and other paired structures are described in the singular, except where the context makes this inappropriate. Label data for specimens taken from cultures will often have two dates: the date the culture was established (*est.*), and the date the specimen eclosed, emerged or was pinned (*ecl.*, *em.*); iso-♀ cultures are established from one wild-caught female, and may be maintained for many generations, the first generation or first filial is F_1 , the second F_2 , etc. Label data is verbatim, line breaks are marked |, countries are omitted if redundant. Live strains originally maintained by the *University of Texas Genetics Foundation* (*Texas Stock Center*) are referred to using the original code numbers with prefix *Texas*.

Taxonomy

In the descriptions of the three new species below, only the characters that differentiate the taxa among the others in the *ananassae* complex or *ananassae* subgroup are presented (Bock & Wheeler, 1972; McEvey *et al.*, 1987). For completeness we have, however, given the full suite of morphometric measures. The following members of the *Drosophila ananassae* species complex, except *D. schugi* sp.nov., closely resemble *D. ananassae* in features of external morphology and male terminalia. They are discussed below to provide a comparative context for the descriptions of *D. pandora* sp.nov. and *D. anomalata* sp.nov.

Drosophila (Sophophora) ananassae Doleschall, 1859

Figs. 6–9, 22–27, 42, 44–45, 60–65, 89, 92

D. ananassae Doleschall, 1859. *Nat. Tijds. Ned. Ind.* 17: 128.
Type locality: Amboina [=Ambon, Indonesia]. Rocha Pité & Tsacas (1980) state that the “holotype” is lost.
Synonyms are given by Brake & Bächli (2008).

General features. As described by Kikkawa & Peng (1938), Patterson (1943), Sturtevant (1916), Wheeler & Takada (1964) and Bock & Wheeler (1972).

Sex comb (Figs. 60–60): Transverse rows on the first 2 tarsal segments. Bock & Wheeler (1972) describe the configuration as: “5 metatarsal rows of (from above down) 2–3, 2–4, 4–6, 5–7, and 5–8 teeth; and 3–4 rows on the second tarsal segment of (from above down) 0–2, 3–4, 3–5, and 3–5 teeth;

a further tooth generally present apically on the third tarsal segment.” Our scores of metatarsal rows (= tarsomere I) are 5–6 rows, starting at proximal end: 0–2, 0–3, 1–6, 3–7, 4–9, and 5–9; and 3–5 rows on the second tarsal segment (= tarsomere II) of 0–1, 0–4, 1–6, 3–6, and 3–7.

Male terminalia (Figs. 6–9, 22–27, 42–45): Epandria have been figured previously by Hsu (1949), Kikkawa & Peng (1938), Malogolowkin (1948), and Wheeler & Takada (1964). A detailed study of the structure and precopulatory function of the spine on the ventral cercal lobe or secondary clasper has been given by (Grieshop & Polak, 2012). Hypandria previously figured by Malogolowkin (1948). We place considerable emphasis on the form of the medial expansion of the novasternum, we regard the “pointed-head” or “pimple-head” shape (seen clearly in Figs. 6–9 cf. Figs. 2–5) as being, among other traits, typical of *D. ananassae*.

Distribution. Worldwide distribution in tropical and subtropical areas (Bock & Wheeler, 1972; Brake & Bächli, 2008). In northeastern and eastern Australia the species is present from Torres Strait through various rainforests of Cape York Peninsula to Cairns, Townsville and as far south as Corindi in NSW (Fig. 1, Appendix 1).

This species has been reported from Darwin and Kakadu in Northern Territory, Australia (Vogl *et al.*, 2003; Das *et al.*, 2004) but we are unable to confirm this. We agree with van Klinken *et al.*, (2002) that it is absent in Darwin; all specimens we have examined from Darwin and rainforests nearby have been *D. pandora* (see below). Indeed van Klinken *et al.* (2002) found that their “*Drosophila* nr *ananassae*” (a probable synonym of *D. pandora*, see below) was the most abundant species at fruit baits in rainforests (68%, $n=742$ ♂♂) and a common species in urban habitats (20%, $n=1131$ ♂♂) (van Klinken *et al.*, 2002).

Specimens examined (see also Appendix 1). The following males have been dissected and determined to be *D. ananassae*. **Mauritius:** ... | Beach Lane, Pereybère 5m | 19.9947°S 57.5928°E ±400m | 17–18.x.2012 fruit trap | John Tann. **Indonesia (Bali):** ... | Mumbul Inn, Ubud | 8.5057°S 115.2608°E | WGS84±100m 15.iv.2011 | S. McEvey & J. Weiner. **Indonesia (Sulawesi):** ... Bantimurung | 5.01720°S 119.68160°E | 26.vi.2012, fruit | S.F.McEvey & J.Weiner. **Indonesia (West Papua):** ... Sabar Miokre | 0.70657°S 135.60072°E | 16.vii.2012 kitchen | S.F.McEvey & J.Weiner; Gam Island | -0.5349° 130.5838° | off fresh lemon | March 2015 [Andrew Davis] AMS K357514. **Australia (Christmas Island):** ... | 10°30'S 105°35'E | 24–30 Nov. 2003 | S.F. McEvey *et al.* **Papua New Guinea (mainland):** PNG Tabubil 570 m | 5.258°S 141.220°E | 3.ii.2009 fruit | Shane F. McEvey. **PNG (Bismarck Archipelago):** PNG, LIHIR ISLAND | New Ireland Province | 3°03'S 152°36'E | October 2001 | M.Moulds & M.Humphrey. **Australia (Queensland):** “QLD Thursday Is [Torres Strait] | 10–11 June 2003 | coll. McEvey, Schug | Gray Smith and Marshall” ♂ AMS K274594, *D. ananassae* det. McEvey & Schiffer, 2013, after dissection and examination of terminalia; “Iron Range, Qld. | fruit bait | 30.iv.1976 | I.R. Bock” 2♂♂ AMS K119306 and K119308, *D. ananassae* det. McEvey & Schiffer, 2013 after dissection; *D. ananassae* iso-♀ strains CBR52, CBR54 and CBR57 established from females collected in fruit-baited traps at Lake Placid in 2011, M. Schiffer in MSRC; “QLD Townsville | Joleka, ... | fruit baited trap | Sept 2011, Code CBN | coll. Michele Schiffer” *D. ananassae* det. M. Schiffer, 2012, in MSRC; 5♂♂, QLD Serina Beach, fruit shed | 6–7 April 2014 | Michele Schiffer CGZ MSRC; the southernmost Australian record is: “Corindi, NSW | 30°0'58"S 153°7'34.8"E | Raspberries | coll. Jennifer Denison [Olivia Reynolds] | 9/4/2010–20/04/2010” 2♂♂ AMS K357521–522, *D. ananassae* det. McEvey, 2015. Specimens from **Australia (Norfolk Island)** (ANIC 29031439–451, det. McE & MS, 2015), unlike those from the Australian mainland, are very darkly pigmented (Bock, 1986). **Vanuatu:** ... Efate, 6km | SW Port Vila, banana | bait, 21–26.viii.2006 | Shane F. McEvey. **Loyalty Islands:** ... | Lifou, We, coast scrub | 4m 1–2.v.2006 banana | S. McEvey & B. Day. **Fiji:** FIJI Viti Levu | 35 km S Nadi | Sigatoka Valley Rd | 20 Oct 2001 mango | Michal Polak. FIJI,

Viti Levu | 1.5km N Sigatoka | swept 10 June 2004 | Shane F. McEvey. FIJI, Viti Levu | Nadi, fruit bait | 8 June 2004 | Shane F. McEvey. **Western Samoa**: ... | Apia 13–14 Jun 2003 | coll. McEvey Schug | Smith & Marshall. **Society Islands**: SOCIETY IS Moorea | Belvédère, 250m | fruit 19 June 2004 | Shane F. McEvey. **Marquesas**: ... Nuku Hiva | 1.5km NW Taipivai | 34m, 4.viii.2007 | swept, S.F. McEvey [& S. Gray Smith].

***Drosophila (Sophophora) monieri*
McEvey & Tsacas, 1987**

Fig. 11

Drosophila (Sophophora) monieri McEvey & Tsacas, 1987:378 (in McEvey *et al.*, 1987). Type locality: Moorea, Society Islands, French Polynesia.

General features. As described by McEvey *et al.* (1987); Fig. 11 (Belvédère, Moorea specimen), shows the distinctive, small, pointed, anterior paramere that distinguishes this species from *D. phaeopleura*. Matsuda *et al.* (2009) establish a close phylogenetic relationship between *D. monieri* and *D. phaeopleura* within the *ananassae* complex.

Distribution. Restricted to Moorea and Tahiti, Society Islands, French Polynesia; we did not identify this species in our collections from the Marquesas islands (Fig. 1).

Specimens examined. The following males have been dissected and determined to be *D. monieri*. **French Polynesia (Society Islands)**: Moorea, Fr Polynesia | type-culture n° 271 | ii.1986, J.R. David; SOCIETY IS Moorea | Belvédère, 250m | fruit 19 June 2004 | Shane F. McEvey.

***Drosophila (Sophophora) ochrogaster*
Chassagnard, 1992**

Fig. 12

Drosophila (Sophophora) ochrogaster Chassagnard, in Chassagnard & Groseille, 1992: 63. Type locality: Col des Roussettes, New Caledonia.

General features. As described by Chassagnard & Groseille (1992); the terminalia of a Mont Koghis (New Caledonia) specimen is pictured in Fig. 12 showing the paramedian setae of the novasternum—almost as long as the anterior paramere (*les soies paramédianes presque aussi longues que les paramères antérieurs*) and the form of the latter: longer than wide, rounded apically, slightly curved toward the aedeagus, carrying 4 sensilla, one of which is apical (*paramères antérieurs plus longs que larges, à apex arrondi, et légèrement courbés vers le phallus, ils portent chacun 4 sensilles dont une apicale*).

Distribution. Restricted to New Caledonia. This species was collected in 2000 (Barker, McEvey, Polak and Starmer) at Mont Koghis in 2000, New Caledonia—voucher specimens in IRD, MNHN and AMS (K282802–808). Collecting on Lifou, one of the Loyalty Islands east of New Caledonia (see Wé in Fig. 1), yielded only *D. ananassae* (hypandrium, Fig. 24).

Specimens examined. The following males have been dissected and determined to be *D. ochrogaster*. **New Caledonia**: ... | Mont Koghis rainforest | 11.ii.2000, coll. Barker | McEvey Polak Starmer; ... | Mt Koghis 490m | 18.iv.2006 swept | S. McEvey & B. Day. [Specimens determined to be *D. pallidosa* from Noumea by Tomimura,

Matsuda, and Tobari (1993) could, on examination of terminalia, be found to be *D. ochrogaster*, but see Matsuda *et al.* (2009), and discussion under *D. pallidosa* below; the *D. pallidosa* in Noumea record is omitted from the Appendix].

***Drosophila (Sophophora) pallidosa*
Bock & Wheeler, 1972**

Figs. 30–32, 47

Drosophila (Sophophora) pallidosa Bock & Wheeler, 1972: 38. Type locality: Fiji.

General features. Indistinguishable from *Drosophila ananassae* except “the reduced number of rows in the sex comb of *pallidosa* in comparison with *ananassae*”—3 to 4 transverse rows on tarsomere I in *D. pallidosa* (compared to 5–6 rows in *D. ananassae*) described as (from proximal end) 0–2, 2–3, 5–6, and 4–7 teeth; and 3 rows on tarsomere II of 1, 3–4, and 3–4 teeth. We have noticed an additional tooth apically on tarsomere III—about 22–23 teeth in total (after Bock & Wheeler, 1972).

Drosophila pallidosa was recognized originally because, in the Fiji–Samoa area, it existed as a pale-form living among dark-form *D. ananassae*. Strains were available for study and compelling evidence of the natural separateness of the two forms was provided by Futch (1966) and Johnson *et al.* (1966b). “Futch (1966), in addition to finding evidence of complete ethological isolation between *ananassae* and *pallidosa* in nature, noted differences in [chromosomal] inversion patterns between the two species.” Johnson *et al.* (1966b) investigated isozyme polymorphisms and found that *ananassae* and “pale form” *ananassae* [= *pallidosa*] have attained different polymorphic balances for a number of enzyme systems.” Their lines of evidence led Bock & Wheeler (1972) to conclude that, despite their failure to find morphological differences in the male terminalia, that the pale or “light” form flies warranted treatment as a new species. This key difference served as a useful indicator but only in Fiji and Samoa. Elsewhere in the Pacific *D. ananassae* existed with both pale and dark abdominal pigmentation. The distribution of these pigment variants was mapped by McEvey *et al.* (1987). In areas where *D. ananassae* presented as “pale” like in New Guinea and Australia, taxonomic uncertainty prevailed.

The outer limits (especially the outer western limits) of the distribution of *D. pallidosa* have never been established. Specimens collected by us in Vanuatu (see Port Vila, Fig. 1), and preserved in the Australian Museum (AMS K275414–423) together with a long series collected by Michal Polak in 2003, have sex combs conforming to the *D. pallidosa* description and—among those that have been dissected—terminalia resembling the *D. pallidosa*/*D. ananassae* form. Matsuda *et al.* (2009, their suppl. table) have determined that *D. pallidosa* occurs in Tonga (Fig. 1) and together with *D. ochrogaster* in Noumea, New Caledonia (Fig. 1). Their NOU88 Noumea *D. pallidosa* strain has low COI sequence divergence from conspecific Fijian and Tongan strains.

The possibility that the pale iso-female lines from Moorea are *D. pallidosa* has been rejected by a careful examination of the sex combs; none were found to have less than 19 teeth on the metatarsus. Thus the material collected in French Polynesia does conform to the description of *D. ananassae*

even though it is polymorphic for abdominal pigmentation. (McEvey *et al.*, 1987).

Distribution. Fiji, Samoa and Tonga. Specimens determined by Bock and Wheeler as belonging to this species are from Fiji and Samoa [Tutuila, Savaii and Upolu]. Tongan specimens of this species have been determined by Tobari's group. Reports of this species from New Caledonia are treated here as incorrect.

Specimens examined. The following males have been dissected and determined to be *D. pallidosa*. **Fiji:** FIJI Lautoka | culture NAN24 | Kyorin University stock k-ae002 | 1981 Fuyama, Takanashi, Tobari | isofemale line; FIJI, Viti Levu | 6km N Sigatoka | fruit 10 June 2004 | Shane F. McEvey. **Samoa:** ... Savaii, Aopo | between 1984 and 1990 | US Dros. Stock Center | 14024-0433.00. **American Samoa:** ... | Pago Pago, Tutuila | Mar–Aug 1962 | Wheeler & Stone US Dros. Stock Center 14024-0433.01.

Drosophila (Sophophora) pandora sp.nov.

Figs. 2–5, 14–21, 35–36, 38–41, 46, 54–59, 90, 96

Drosophila “papuensis-like” of Tomimura *et al.* (1993); Matsuda *et al.* (2009).

Drosophila nr *ironensis*, van Klinken, 1996, p. 247; van Klinken & Walter, 2001, pp. 168, 176 [north Queensland and Northern Territory].

Drosophila nr *ananassae*, van Klinken *et al.*, 2002, p. 238 [Northern Territory].

Distinguishing features

Drosophila pandora sp.nov. can be distinguished by reference to the elongate, straight, basal extension of the anterior paramere, the “viking-helmet” shape of the convexity of the caudal margin of the novasternum, the overall quadrate and relatively wide profile of the combined aedeagus plus posterior parameres, the presence of an acuminate kink on the bend in the anterior paramere, and the configuration, and number, of teeth in sex combs on the male foreleg.

Description (♂)

Types. Holotype ♂, AMS K357344, McEvey 31861, from type culture CAQ408: “QLD Lake Placid, alt. 17m | -16.870° 145.676° WGS84 | [culture established by M. Schiffer from rainforest, fruit-baited, iso-♀] ix.2011, [specimens eclosed, generation F₄₁] ii.2014 | Schiffer, ex culture CAQ408 [culture maintained at the University of Melbourne]”. Paratypes (70♂♂ and 35♀♀, registered McEvey 31855–860 and McEvey 31862–960, all from type culture with same label-data as holotype): 35♂♂ (K357339–343, K357345–374), and 21♀♀ (K357375–395) in Australian Museum, Sydney; 5♂♂ and 2♀♀ in each of the following museums (with McEvey's registration numbers): American Museum of Natural History, New York (AMNH, McE31855, 31892–895♂♂, McE31937–938♀♀); Australian National Insect Collection, Canberra (ANIC 29031663–667♂♂ [McE31896–900♂♂], ANIC 29031668–669♀♀ [McE31939–940♀♀]); Museum Zoologicum Bogoriense, Bogor (MZB, McE31901–905♂♂, McE31941–942♀♀); Kunming Institute of Zoology, Chinese Academy of Science, Kunming (KIZ, McE31906–910♂♂, McE31943–944♀♀); National Science Museum, Tokyo

(NSMT, McE31911–915♂♂, McE31945♀, McE31956♀); Queensland Museum, Brisbane (QMB, McE31946–950♂♂, McE31957–958♀♀); and United States National Museum, Washington, D.C. (USNM, McE31951–955♂♂, McE31959–960♀♀). Living flies from type culture CAQ408 have been sent to the *Drosophila Genetic Resource Center* (Kyoto) and the *Drosophila Species Stock Center* (San Diego).

Body length. 2.2 mm ♂.

Head. Arista with four rays above and two to three below, plus terminal fork. Orbital setae in ratio 2:1:2. Measurements of holotype ♂—BL(McE) = 2.17 mm, BL(Z&T) = 1.63 mm, hw/fw(ov) = 1.91, hw/fw(iv) = 2.29, hw/fw(vt) = 1.99, hw/fw(a.r.orb) = 2.20, hw/fw(a.oc) = 2.04, hw/fw(ptl) = 2.61, fw(ov)/fl = 1.57, fw(iv)/fl = 1.31, fw(vt)/fl = 1.51, fw(a.oc)/fl = 1.48, fw(a.r.orb)/fl = 1.36, p.r.orb = 0.99, rc.orb = 0.48, proc.orb/a.r.orb = 2.05, oc/proc.orb = 1.08, pv/oc = 0.76, p.r.orb/iv = 0.73, orbito-index = 0.76, vt-index = 1.05, oc-gap/pv-gap = 0.44, o/j = 12.00, ch/o = 0.10, o/ow = 1.32, svb/vb = 0.65, flw = 1.51, avd = 0.93, adf = 1.96, arista free ends = 8–9.

Thorax. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex comb of male foreleg (Figs. 54–59, Tables 1 and 2) in 2–6 transverse rows on tarsomere I of (from above down) 0–1, 0–2, 0–3, 0–6, 2–8, and 3–8 teeth; and 2–4 rows on tarsomere II of 0–2, 0–4, 1–6, and 2–8 teeth. Other thoracic measurements: bsc/asc = 0.90, sterno-index = 0.55, m/a.kepst = 0.60, p.kepst/pdc = 1.06, pdc/asc = 0.93, asc-bsc/asc-asc = 1.21, a-pdc/dc-gap = 0.39, adc/pdc = 0.61, fw(a.oc)/dc-gap = 1.32.

Wing. Hyaline, wing length c. 1.8 mm. L(Ax) = 1.76 mm, WL = 1.51 mm, L₁ = 1.33 mm, L(Ax)/WW = 2.31, WL/WW = 1.98, L₁/WW = 1.75, C-index = 1.54, 4v-index = 2.56, 4c-index = 1.75, 5x-index = 2.29, M-index = 0.89, ac-index = 3.26, C3 fringe = 0.54.

Abdomen (Fig. 96). Tergites of both sexes with diffuse, dark, narrow bands posteriorly, fainter posterolaterally. Setae of T5 and T6 generally pointing caudally (cf. *D. ironensis*, Figs. 94–95).

Male terminalia. *Epandrium* (*periphallic organs*) (Figs. 38–41). Genital arch narrow dorsally and broad laterally; toe (ventral epandrial lobe) elongate as in *D. ananassae*, with about 6–8 setae. Primary and secondary claspers present. Primary clasper (surstylus) large with an inner or median row of 5–6 strong setae that merges into a cluster of an additional 8–9 setae (one large) and two series of short, blunt, thick teeth (prensisetae) laterally. The upper series has 5–6 prensisetae, the lower series has 2–3 of similar form. The secondary clasper (ventral cercal lobe) is very small with a very large curved, black, medial tooth, and with several small setae.

Hypandrium (*phallic organs*). (Figs. 2–5, 14–21, 35, 36). The medial expansion of the novasternum (*n* in Fig. 4) resembles a “viking helmet”—rounded like the crown of a human head with the submedian spines arising like “horns” laterally. Aedeagus non-bifid, apically hirsute. Anterior parameres small, digitiform with large apical seta and several medial sensilla (*ap* in Fig. 4) and with a hugely extended and recurved structure at its base—the basal extension (*bx* in Fig. 4). The basal extension terminates as a very long, pointed and

sclerotized appendage (Figs. 2–4); in ventral view, the lateral side of this caudally extended structure is almost straight, the other side curves near the tip (cf. *D. ananassae*—basal extension tapers on both sides toward a pointed tip, e.g., Figs. 6, 8). The basal extension pivots outwards (e.g., Fig. 16) when the aedeagus extends. It is figured in the resting or not-outwardly-pivoted position in Fig. 4. An acuminate kink in the “bend” of the anterior paramere (*ak*, Fig. 4) is visible in ventral view (Figs. 2–5, 14–21, this kink is absent in *D. ananassae* e.g., Figs. 6–9, 22–25). Posterior paramere long, extending beyond aedeagus; slender, tapering to a point, bending abruptly (cf. gradually in *D. ananassae* and *D. pallidosa*) at apex of aedeagus and sheathing it. The overall “sheathed” phallus width is about 0.4 of the hypandrium width in *D. pandora* and smaller, c. 0.3, in *D. ananassae* (compare Figs. 2–5 and Figs. 6–9). The transverse band (*tb* Fig. 4) of the ventral phragma is short (cf. long in *D. ananassae*) and opens into a lateral deltoid-shaped expansion (*lx* Fig. 4, versus not expanded in *D. ananassae*, e.g. Figs. 6, 23).

Female. Difficult to identify except by extrapolation from male siblings or progeny.

Female terminalia. Oviscapt concolorous with tergite VI (Fig. 90).

Specimens examined. **Australia (Western Australia):** 1♂, ... -16.3604°S 124.7684°E | Northwest Kimberley | MALAISE-trap sample (7 days) | Coll: M21/2E2rb (29Jan2013) | O.R. Edwards & R.K. Didham CSIRO (WAM). **Australia, Northern Territory:** 3♂♂, NT Holmes Jungle | -12.3978° 130.9345° ±50m | 21.v.2013 swept | S.F. McEvey & G.R. Brown | AMS K357515–517; 3♂♂, *ibid* | 22.v.2013 swept | S.F. McEvey & G.R. Brown | AMS K357518–520. **Australia (Queensland):** 2♂♂, | AMS K194455–456 | Gordon Ck, Iron Range | 12°43'S 143°19'E N.Qld | swept over flowers at | rainforest fringe | 12.v.1981 S.F. McEvey; 1♂, QLD Lake Placid | -16.8678° 145.6731° ±50m | est. ix.2011, em. 22.i.2013 | M. Schiffer culture CAR274; 2♂♂, *ibid* | M. Schiffer culture CAQ408; 1♂, *ibid* | M. Schiffer culture CAQ425; 1♂, | AMS K274605 | McE9362 | QLD, Heathlands | Bertie Creek pump | 11:46S 142:36E fruit | 13.3.92 S.F. McEvey; 2♂♂, | AMS K274602–603 | McE9156, McE9162 | QLD, Heathlands | Bertie Creek pump | 11:46S 142:36E fruit | 10.iii.92 S.F. McEvey; 1♂, QLD Townsville | Tucson stock 14024-0371.11 | Kyorin University stock k-aat001; 1♂, QUEENSLAND | culture AUS52 | Kyorin University stock k-aat002 | M. Hatsumi | iso-♀ line; 1♂, QLD Black River | ... Vivian Voss Crt | 11 April 2014 fruit bait | Michele Schiffer; 1♂, QLD Mango Tree Tourist Pk | Innisfail, orange trees | 13–14 April 2014 fruit bait | Michele Schiffer; 4♂♂, QLD Serina Beach, fruit shed | 6–7 April 2014 | Michele Schiffer CGZ MSRC; 32♂♂, QLD Rockhampton, orchard | 2 April 2014 | Michele Schiffer CGW MSRC. **Australia (Torres Strait islands):** 1♂, ANIC 29031424 | Thursday Is., NQ | fruit (domestic) | 15.i.1980 | S.F. McEvey; 2♂♂, ANIC 29031431–432 | Moa Island, N. Qld | fruit (domestic) | 2.ii.1980 | S.F. McEvey. **Papua New Guinea:** 2♂♂, PNG Wanigela | 9°16'S 149°08'E | 12–28 Feb 2003 | Shane F. McEvey; 2♂♂, PNG Tabubil 570 m | 5.258°S 141.220°E | 3.ii.2009 fruit | Shane F. McEvey; 1♂, Wau, Papua New Guinea | culture WAU142 | 1981 | Kyorin University stock k-aat003 | E. Takanashi, Y. N. Tobari | iso-♀ line.

Distribution (Fig. 1). This species is known from across tropical Australia (to as far south as Rockhampton in the east and The Kimberley in the west) and eastern New Guinea (from Tabubil, Wanigela, Wau, Lae and Port Moresby).

Etymology. The proposed name *pandora* is a noun from the contemporary phrase *to open Pandora's Box* which, in turn, is from Ancient Greek mythology. By investigating the possibility that two or more species co-exist where previously it was thought only *Drosophila ananassae* occurred, we felt that we were opening a taxonomic Pandora's Box, replacing simplicity with complexity.

Remarks

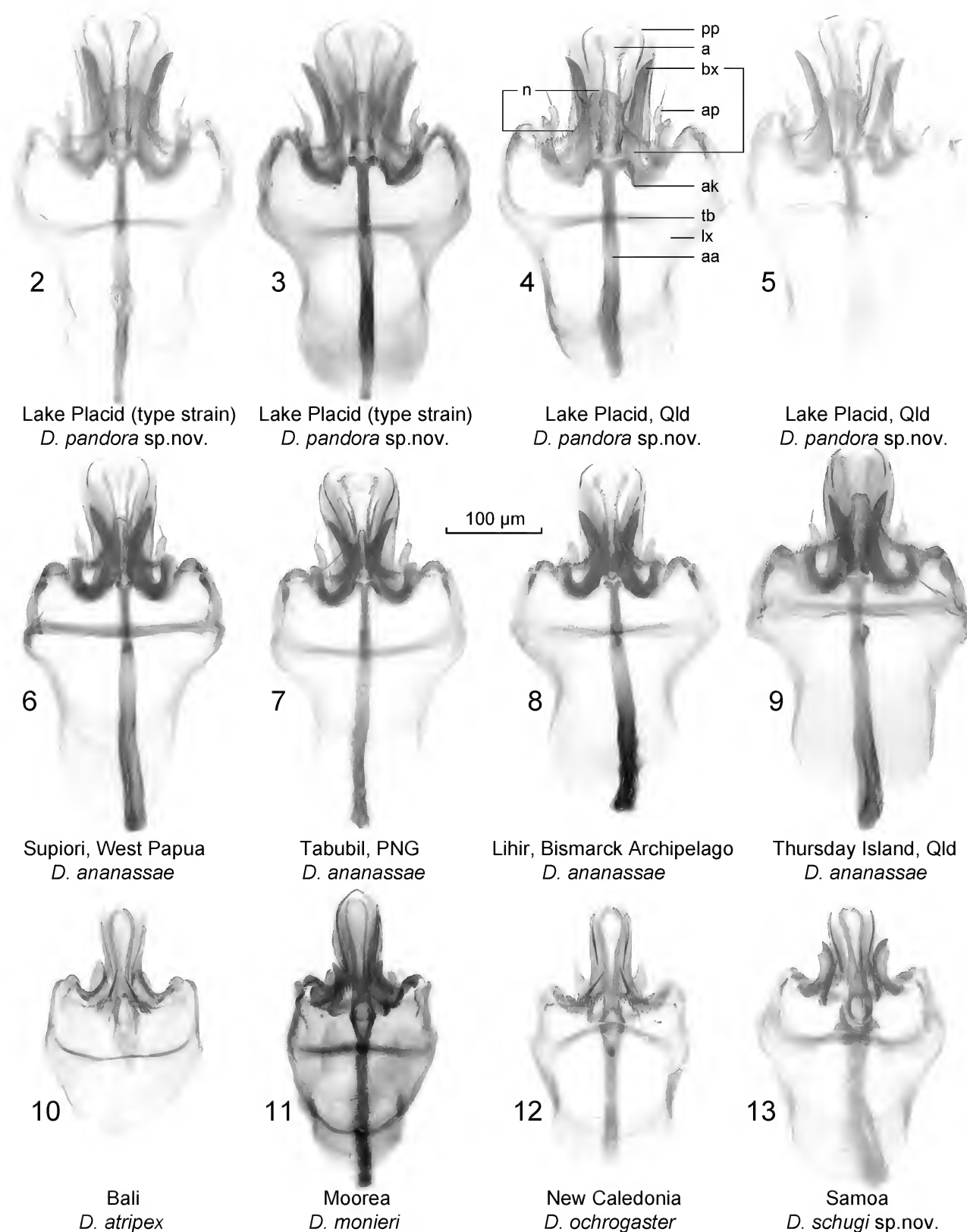
This species has, since the 1970s, been confused in Australia with *Drosophila ananassae*, see, for example, Bock (1977); Parsons & Bock (1979, p. 230); Tribe & Bock (1981); McEvey (1982); McEvey & Bock (1982); and Schug *et al.* (2007). The two species are exceedingly similar in overall coloration but with experience one can detect that *D. ananassae* is slightly larger and darker. The sex combs of male forelegs are a useful indicator (Figs. 54–65). Table 2 shows that the average total number of teeth in all combs of one leg is about 22 in *D. pandora* and about 37 in *D. ananassae*. However, the most reliable diagnostic characters are found in the male hypandrium.

By examination of terminalia we have determined that *D. pandora* is not synonymous with *Drosophila ananassae* from Norfolk Island (Bock & Parsons, 1981), with *Drosophila “pallidosa-like”* of Tomimura *et al.* (1993, p. 147), or with *Drosophila “pallidosa-like Wau”* of Matsuda *et al.*, 2009:159.

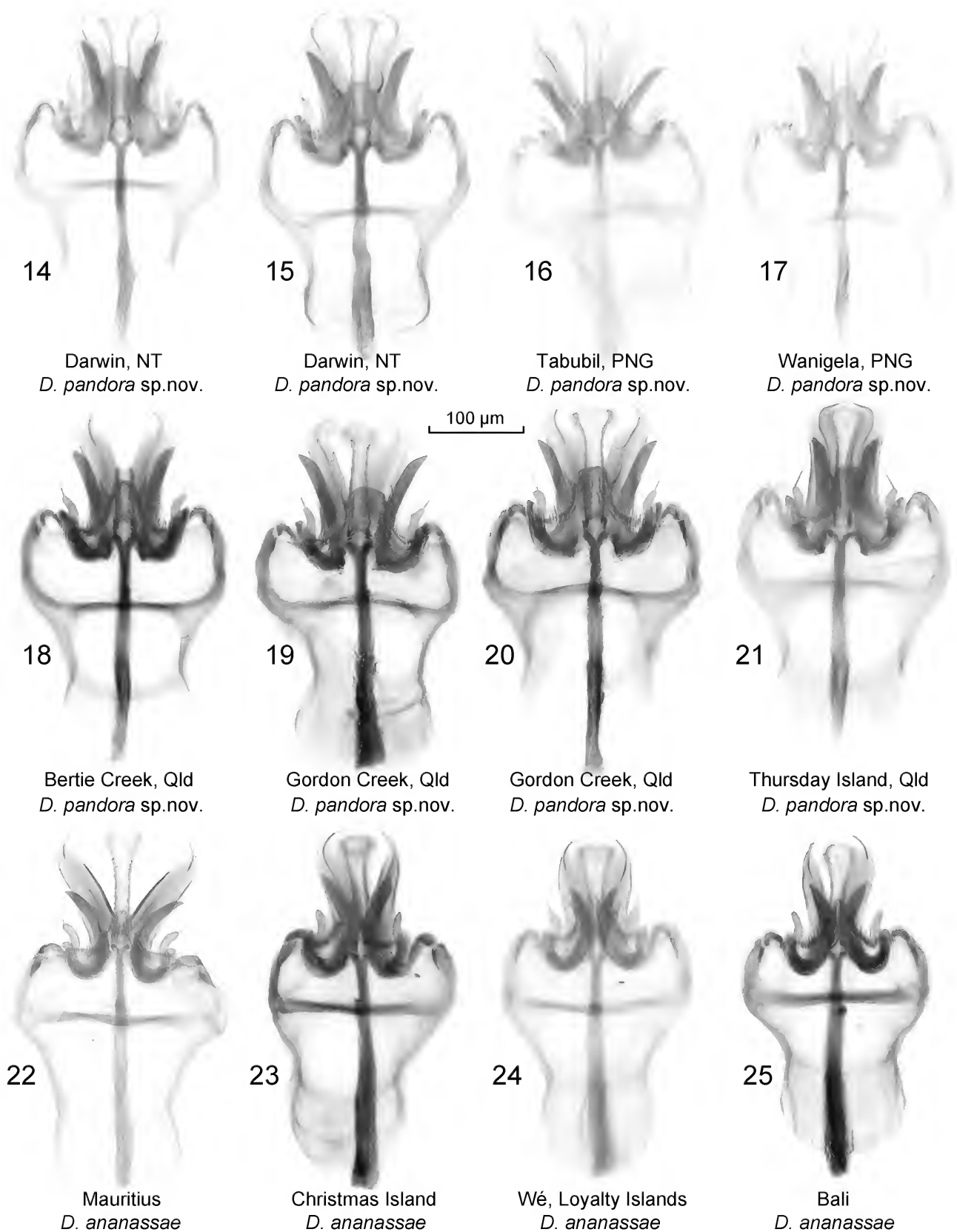
We have excluded *D. atripex* Bock & Wheeler, 1972 (Fig. 10) as a possible synonym by examining specimens from Thailand (THAILAND Pak Chong | 14°41'N 101°24'E | 1–15.vii.1989 | coll. J.R. David) and Bali (INDONESIA, BALI | Mumbul Inn, Ubud | 8.5057°S 115.2608°E | WGS84±100m 15.iv.2011 | S. McEvey & J. Weiner). *Drosophila pandora* is not synonymous with the species under culture as “*pallidosa-like*”(NEW GUINEA Lae | culture LAE345 | Kyorin University stock k-aau001 | 1981 | E. Takanashi, and Y.N. Tobari | iso-♀ line), Takanashi, Tobari and others, treat this strain as not “*papuensis-like*” (i.e. not *D. pandora*). We have examined males from two strains of *Drosophila “pallidosa-like WAU”* (Fig. 37) (NEW GUINEA Bulolo | culture Bulolo79-2 | Kyorin University stock k-aav002 | 1979 H.L. Carson, T. Okada | iso-♀ line; and Wau, Papua New Guinea | culture WAU92 [1981] | Kyorin University stock k-aav001 | E. Takanashi, Y. N. Tobari | iso-♀ line) and found it not to be synonymous with *D. pandora*.

The species is easily reared in the laboratory. Future studies of this and other species in this complex should consider depositing male voucher specimens in a museum in order that links can confidently be made between genetic, genomic, cytological, behavioural and other experimental findings and taxonomy which is still based largely on morphology.

At Iron Range (Fig. 1) van Klinken reared “sp. nr *D. ironensis*” (a likely synonym of *D. pandora*) from fruits of the following plants: *Mangifera indica*, *Ptychosperma elegans*, *Garcinia riparia*, *Momordica charantia*, *Elaeocarpus arnhemicus*, *Ficus nodosa*, *Syzygium bamagense*, *Morinda citrifolia*, *Nauclea orientalis* and three other unidentified fruits (van Klinken & Walter, 2001). In rainforests around Cairns he reared *D. pandora* from fruit of the following species: *Barringtonia calypttrata*, *Elaeocarpus angustifolius*, *E. bancroftii*, *Gmelina* sp., *Polyalthia michaelii*, *Polyscias* sp., *Randia fitzalani*, *Syzygium cormiflorum*, and two unidentified spp. In Northern Territory, around Darwin, *D. pandora* (det. as “sp. nr *D. ironensis*”) was reared from fruit of: *Averrhoa carambola*, *Citrus aurantifolia*, *C. reticulata*, *Citrus* sp., *Malphighia glabra*, *Mammea americana*, *Manilkara zapota*, *Nauclea orientalis*, *Psidium catteliamum*, *P. guajava*, *Spondia cytherea*, *S. mombin*, and *Terminalia* sp. (van Klinken & Walter, 2001).



Figures 2–13. Hypandria of species of the *Drosophila ananassae* subgroup. *Drosophila pandora* sp.nov. from Lake Placid, northern Queensland, (2–3) type strain = iso-♀ strain CAQ408, (4) iso-♀ strain CAQ425, (5) iso-♀ strain CAR274. *Drosophila ananassae* from (6) Supiori, West Papua; (7) Tabubil 750m, Western Province, Papua New Guinea; (8) Lihir, Bismarck Archipelago, New Ireland Province, PNG; (9) Thursday Island, Torres Strait, northern Queensland. *Drosophila atripex* (10) Ubud, Bali, Indonesia. *Drosophila monieri* (11) Belvédère 250 m, fruit bait, Moorea, Society Islands, French Polynesia. *Drosophila ochrogaster* (12) Mont Koghis, New Caledonia. *Drosophila schugi* sp.nov. (13) Malololelei, Upolu, Samoa (paratype AMS K282923). Abbreviations: *a*, aedeagus; *aa*, aedeagal apodeme; *ak*, acuminate kink of anterior paramere (cf. featureless curve, e.g. Figs. 7–9, 22–25); *ap*, anterior paramere; *bx*, basal extension of anterior paramere; *lx*, lateral deltoid expansion of transverse band; *n*, novasternum, medial expansion; *pp*, posterior paramere; *tb*, transverse band. Localities—see Fig. 1 and Appendix 1; all specimens in Australian Museum.



Figures 14–25. Hypandria of *Drosophila pandora* sp. nov. and *D. ananassae*. *Drosophila pandora* sp. nov. (14–15) Holmes Jungle, Darwin, Northern Territory; (16) Tabubil 750 m, Western Province, Papua New Guinea; (17) Wanigela, Oro Province, Papua New Guinea; (18) Bertie Creek pump, near Heathlands Homestead, northern Queensland; (19–20) Gordon Creek nr Cooks Hut, Iron Range, northern Queensland; (21) Thursday Island, Torres Strait, northern Queensland. *Drosophila ananassae* (22) Beach Lane, Mauritius; (23) Christmas Island, Indian Ocean nr Java; (24) Wé, Loyalty Islands; (25) Ubud, Bali, Indonesia. Localities mapped in Fig. 1; all specimens in Australian Museum.

***Drosophila (Sophophora) parapallidosa*
Tobari, in Matsuda & Tobari, 2009**

Fig. 34

Drosophila (Sophophora) parapallidosa Tobari, 2009: 135–140, in Matsuda & Tobari (2009).

Drosophila (Sophophora) parapallidosa Tobari, 2009: 157–162, 164, 166, 167 and unpaginated Appendix A, Supplementary material, in Matsuda *et al.* (2009). **Unavailable.**

A description of *Drosophila parapallidosa* has been published twice, once in the journal *Fly* and once in *Drosophila Information Service*. Both works have also been published online. If the print versions fulfilled the regulations of *The Code* (1999) the name proposed in the more recent print version would be treated as *preoccupied*. The *Fly* publication is probably the earlier or older print version, however, it *lacks explicit fixation of a holotype for Drosophila parapallidosa* (see *The Code*, Article 16.4.1) and the description of *Drosophila parapallidosa* in *Fly* is thus invalid—the name proposed therein is *unavailable*. The two online versions can both be discounted because they lack *ZooBank* registration. Of all four taxonomic treatments only one is valid: the print version of the paper in *DIS* Tobari, in Matsuda & Tobari, 2009: 135 (print version). [It is assumed that the print version of *DIS* 92 was published before 31 December 2009, not after. If published in print in 2010, however, the correct authority and year for this species would be Tobari, 2010, in Matsuda & Tobari, 2010].

Drosophila parapallidosa is reported from Kota Kinabalu (Malaysia), Lanyu (Taiwan) and Okinawa (Japan) (Fig. 1). Specimens have been obtained from the Kyorin University stock center and dissected. The terminalia is quite unlike *D. pandora* sp. nov. (Matsuda & Tobari, 2009: fig. 1A; and present work Fig. 34).

Distribution. Malaysia (Kota Kinabalu), Taiwan and Japan.

Specimens examined. The following males have been dissected and determined to be *D. parapallidosa*. **Malaysia:** MALAYSIA Kota Kinabalu | Kyorin University stock k-aas | 1979 see Tomimura *et al.*, 1993 | isofemale lines | Y. Fuyama, F. Hihara, and T.K. Watanabe.

***Drosophila (Sophophora) anomalata* sp. nov.**

Figs. 50–52, 72–81, 91, 93

Types. Holotype ♂, AMS K357034, Schiffer 51016, “[Australia] QLD nr Deeragun 16km W of | Townsville, alt. 16 m | -19.2410° 146.6644°±50m | F8 from iso-♀ type culture | CHC221 establ. 16.iv.2014 | Michele Schiffer 21.xi.2014”. Paratypes (14♂♂, 5♀♀): K357032–033♂♂, K357035–046♂♂, K357047–051♀♀, all same data as holotype, also taken from the type culture 21.xi.2014, all in the Australian Museum. Type culture Schiffer CHC221.

Distinguishing features. Sex combs of male forelegs developed on tarsomere I and II, usually only in 2 rows (rarely 3) on tarsomere I of 1–3 and 4–7 teeth, and in 2–3 rows on tarsomere II of 0–2, 2–4 and 3–4 teeth; female oviscapt darkly pigmented; males bob up and down vigorously in front of and facing females during courtship.

Description (♂)

Body length. 2.3 mm ♂.

Head. The colouration and shape of the head, the eyes and the front, together with the chaetotaxy resemble *D. ananassae*. Measurements of holotype ♂: BL(McE) mm = 2.35; BL(Z&T) mm = 1.63; hw/fw(ov) = 1.84; hw/fw(iv) = 2.31; hw/fw(vt) = 1.80; hw/fw(a.oc) = 2.00; hw/fw(a.r.orb) = 2.09; hw/fw(x.r.orb) = 2.05; hw/fw(ptl) = 2.40; fw(ov)/fl = 1.53; fw(iv)/fl = 1.22; fw(vt)/fl = 1.56; fw(a.oc)/fl = 1.41; fw(a.r.orb)/fl = 1.38; fw(vt)/fw(ptl) = 1.33; p.r.orb = 1.01; rc.orb = 0.39; proc.orb/a.r.orb = 2.57; oc/proc.orb = 1.04; pv/oc = 0.75; p.r.orb/iv = 0.70; orbito-index = 0.63; vt-index = 1.10; oc-gap/pv-gap = 0.50; o/j = 14.13; ch/o = 0.09; o/ow = 1.22; svb/vb = 0.78; flw = 1.32; avd = 0.89; adf = 1.70. Arista with 4–5 dorsal rays and 3–4 ventral rays plus a terminal fork; c.11 free ends.

Thorax. Acrostichal hairs in 8 rows in front of dorsocentral bristles, 4–6 rows between dorsocentrals. Ratio anterior/posterior dorsocentrals 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex comb of male foreleg (Figs. 72–77, Tables 1 and 2) developed on first two tarsal segments, usually only in 2 rows (rarely 3) on tarsomere I of 1–3 and 4–7 teeth, and in 2–3 rows on tarsomere II of 0–2, 2–4 and 3–4 teeth. The average total number of teeth in all sex combs on one leg is 14.5 (range 12–20, Table 2). Other thoracic measurements of holotype: bsc/asc = 0.87; sterno-index = 0.53; m/a.kepst = 0.59; p.kepst/pdc = 1.07; pdc/asc = 0.90; asc-bsc/asc-asc = 1.18; a-pdc/dc-gap = 0.45; fw(a.oc)/dc-gap = 1.36.

Wing. Hyaline. Holotype (average, minimum–maximum): C-index = 1.68 (1.59, 1.42–1.70); 4v-index = 2.15 (2.22, 2.09–2.35); 4c-index = 1.47 (1.55, 1.43–1.66); 5x-index = 1.91 (1.96, 1.74–2.30); ac-index = 3.00 (3.13, 2.90–3.56); M-index = 0.74 (0.77, 0.74–0.84); prox.x = 0.72 (0.90, 0.68–1.28); C3F = 0.52 (0.52, 0.49–0.54); L(Ax) = 1.95 (1.99, 1.91–2.07); WL = 1.66 mm (1.70, 1.64–1.78); L₁ = 1.61 mm (1.64, 1.58–1.73); width = 0.82 mm (0.84, 0.81–0.88).

Abdomen. Tergites of both sexes with diffuse, dark, narrow bands posteriorly, fainter posterolaterally.

Male terminalia. *Epandrium (periphallial organs)* (Figs. 50–52). Genital arch narrow dorsally and broad laterally; toe (ventral epandrial lobe) elongate as in *D. ananassae*, with about 6–8 setae. Primary and secondary claspers present. Primary clasper (surstylus) large with an inner or median row of 4–5 strong setae that merge into a cluster of an additional 8–9 setae (one large) and two series of short, blunt, thick teeth (prensissetae) laterally. The upper series has c.5 prensissetae, the lower series has 3–4 of similar form. The secondary clasper (ventral cercal lobe) is very small with a very large curved, black, medial tooth, and with several small setae.

Hypandrium (phallic organs) (Figs. 78–81). Anterior parameres small, digitiform with large apical seta and several medial sensilla and with a hugely expanded and recurved structure at its base—the basal extension (see *bx* in Fig. 4). The basal extension terminates as a long, pointed and sclerotized appendage; in ventral view, both sides (cf. lateral side only in *D. pandora*), of this caudally extended structure are curved, similar to *D. ananassae*—basal extension tapers on both sides toward a pointed tip,

e.g. Figs. 6, 8). The basal extension pivots outwards when the aedeagus extends. It is figured in the resting or not-outwardly-pivoted position in Figs. 78–81. An acuminate kink in the “bend” of the anterior paramere (*ak*, Fig. 4) is absent as in *D. ananassae* (cf. present in *D. pandora*). Posterior paramere long, extending beyond aedeagus; slender, tapering to a point, curving gradually not bending abruptly at apex of aedeagus and sheathing it. The overall “sheathed” phallus width is about 0.3 of the hypandrium width as in *D. ananassae*.

Female. Oviscapt darkly pigmented (Fig. 91, 93), otherwise difficult to correctly distinguish from *D. ananassae*, *D. pallidosa*, *D. pandora* etc., except by extrapolation from male siblings or progeny.

Distribution. Known only from four Queensland localities: Deeragun garden, Mango Tree Innisfail site CHE, Lake Placid [gardens and buildings], and Lake placid, rainforest remnant (see Appendix 1).

Etymology. The name for this species is a reference to the puzzling interrelationship of this species and the others of the *ananassae* complex in Australia. The morphological data, the hybridization data and the behavioural data are unexpected and anomalous.

Remarks

During the present study males from Deeragun garden, Mango Tree Innisfail site CHE and Lake Placid were found to have very weak sex combs, with a total number of teeth less than 20 (Table 2), yet upon dissection, these males were found to have genitalia indistinguishable from *D. ananassae*. *Drosophila ananassae* and *D. pandora* have different male terminalia but slightly overlapping sex comb metrics, whereas *D. ananassae* and *D. anomalata* differ greatly in sex comb configuration but have similar terminalia. Several live cultures of *D. anomalata* were established from iso-♀♀ collected at two of these three localities: Schiffer strain CHC221 from Deeragun garden, 9–11 Apr. 2014, and strains A5, A25, A29, A41, A43 and A209 from Lake Placid, 4–9 Nov. 2014. Females have distinctly blackened oviscapt compared to *D. pandora*, *D. ananassae*, *D. ironensis*, *D. bipectinata*, and *D. pseudoananassae*. There is a degree of infertility and unviability in crosses between *D. pandora*, *D. anomalata* and *D. ananassae* that cannot be attributed to *Wolbachia* (Tables 3–5). Males of this species display a very distinctive bobbing behaviour while in front of and facing females during courtship. Spieth (1966:137) reported this exceptional behaviour, or one very similar, in strains from Popondetta (Texas 3021.3), Brown River (Texas 3020.9) and Queensland (Texas 2372.11, see comments above relating to this strain). Further work on the courtship behaviour of these species is clearly warranted and likely to be fruitful given recent advances in digital photography. Additionally, Crossley (1986) has found a range of song profiles made by males (with their wings) early and late in the courtship cycle in the *ananassae* subgroup. So courtship display and courtship song are likely to be insightful avenues for future investigation.

The combination of (*a*) morphological characters (sex combs and oviscapt), (*b*) differences in sexual behaviour and (*c*) negative heterosis after hybridization with related

species, compel us to conclude that *D. anomalata* is yet another species that exists in the *ananassae* complex in northern Queensland. The possibility that this species is *D. pallidosa* is rejected because the blackened oviscapt would have been detected by Bock & Wheeler (1972) during their careful search for distinguishing traits among this complex of species. Furthermore, the *Drosophila pallidosa* strain *k-aae002* (*NAN24*) from Lautoka, Fiji (Kyorin University stock) have females with pale, not blackened, oviscapt and 3 sex combs on tarsomere I of 2–3, 5, 5–6 teeth, and 3 combs on tarsomere II of 3, 4, and 4–5 teeth (23–26 teeth in total). The *D. pallidosa* stocks 14024-0433.00 and 14024-0433.01 (from the Drosophila Species Stock Center, San Diego), have females with pale oviscapt and males with sex comb teeth in the arrangement (from proximal end): 0–1, 2, 5, 5–6 (tarsomere I), 1, 3, 4 (tarsomere II) and, interestingly, 1 on tarsomere III; these values are at the upper end of the normal distribution for *D. anomalata*.

Drosophila (Sophophora) schugi sp.nov.

Figs. 13, 49, 53, 66–71, 82–88

Types. Holotype ♂, AMS K282922, McEvey 21326, “WESTERN SAMOA | Malololelei, Upolu | 14–17 June 2003 | coll. S.F. McEvey [with M. Schug, Shelly Gray-Smith, M. Marshall]”. Paratypes (12♂♂), 8 pinned AMS K282919–921, K282923–925, K282929–930; 4 in alcohol AMS K356976–979 (terminalia dissected); all same data as holotype. No cultures established. Terminalia of K282923 dissected and mounted on slide. All in the Australian Museum.

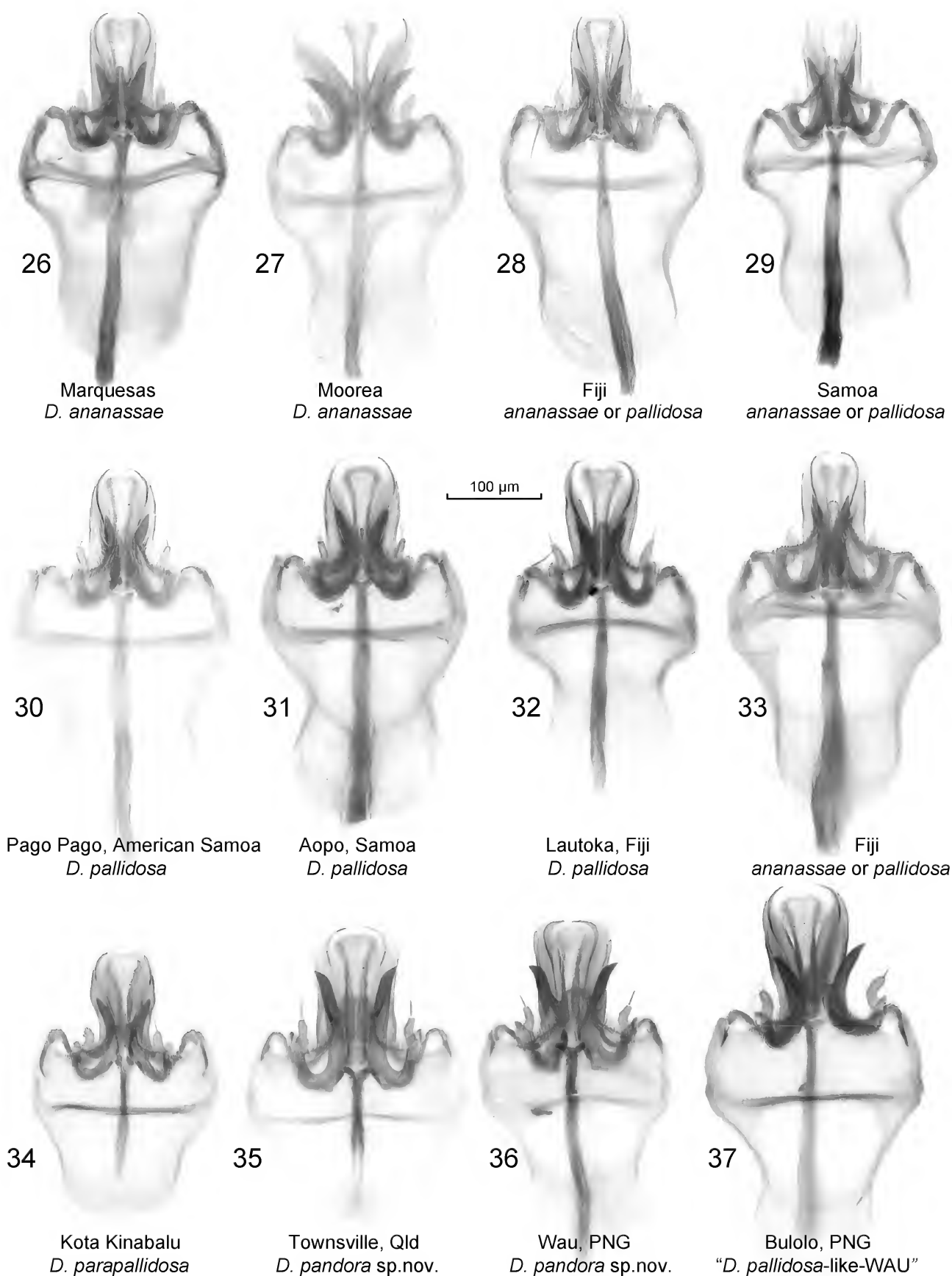
Distinguishing features. Sex combs of male forelegs very strongly developed on first three tarsal segments, tarsomere III in two rows of 2–4 teeth each; anterior parameres large, scimitar-shaped or with ragged lateral edge; caudal margin of novasternum with no medial convexity.

Description (♂)

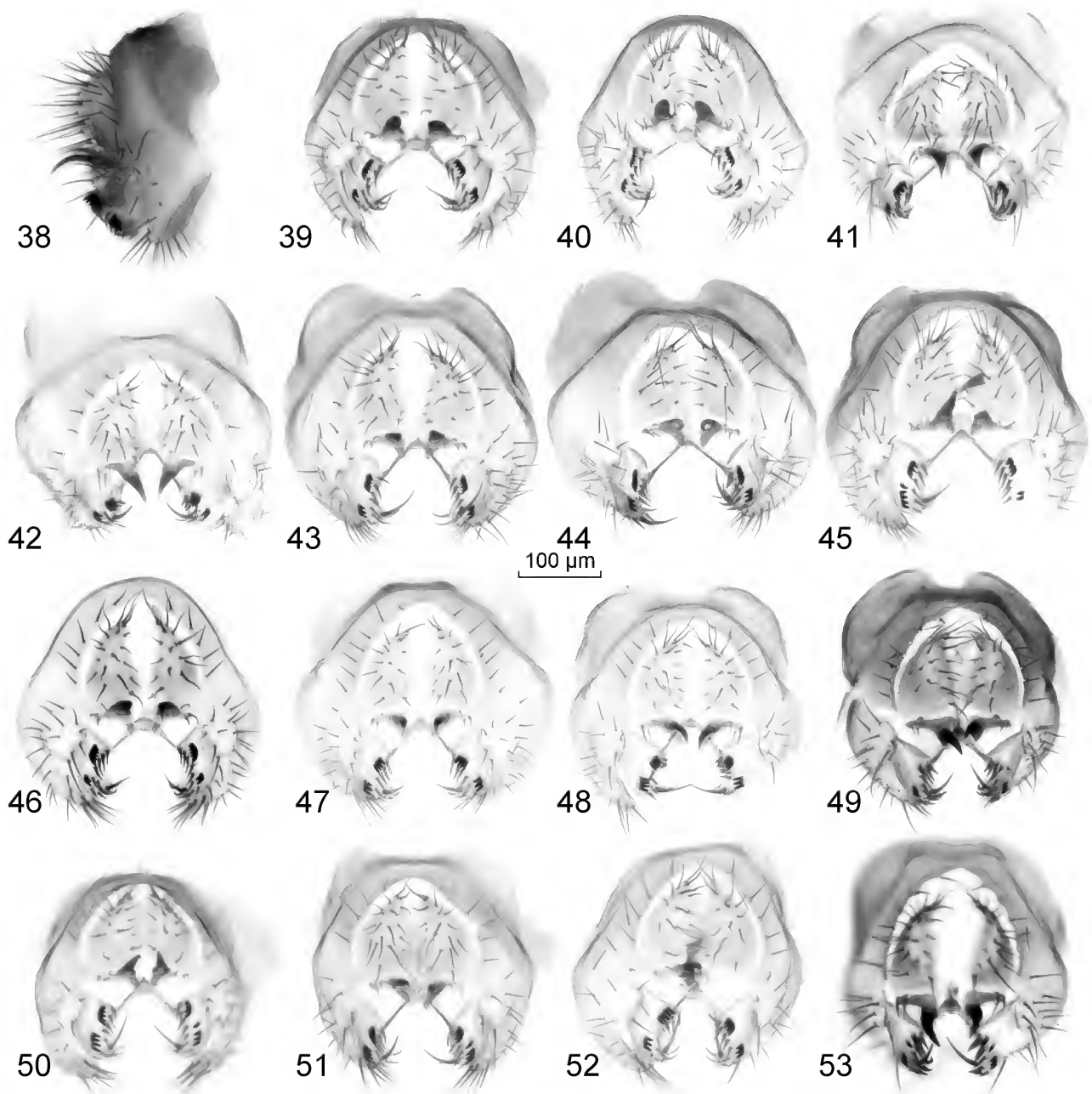
Body length. 2.2 mm ♂.

Head (Fig. 72–74). Arista with 4 rays above and 2–3 below, plus terminal fork. Orbital setae in ratio 4:2:5. Carina (Fig. 72, 74) prominent, dorsally with narrow ridge. Frons narrow anteriorly, broad posteriorly. Greatest width of gena less than 0.1 greatest diameter of eye. (Measurements of holotype ♂)—BL(McE)=2.19 mm, BL(Z&T)=1.58 mm, hw/fw(ov)=1.93, hw/fw(iv)=2.28, hw/fw(vt)=1.91, hw/fw(a.oc)=2.07, hw/fw(a.r.orb)=2.34, hw/fw(ptl)=2.62, fw(ov)/fl=1.33, fw(iv)/fl=1.13, fw(vt)/fl=1.35, fw(a.oc)/fl=1.25, fw(a.r.orb)/fl=1.10, prorb=0.85, rcorb=0.47, proc.orb/a.r.orb=1.83, oc/proc.orb=1.13, pv/oc=0.75, p.r.orb/iv=0.74, orbito-index=0.96, vt-index=1.04, oc-gap/pv-gap=0.44, o/j=29.0, ch/o=0.05, o/ow=1.29, svb/vb=0.89, flw=1.45, avd=0.99, adf=1.66, arista free ends=9.

Thorax. Acrostichal hairs in 8 rows in front of dorsocentral bristles. Ratio anterior/posterior dorsocentrals 0.6. Preapical bristles on all tibiae; apicals on first and second tibiae. Sex comb of male foreleg (Figs. 50–55, Table 1) in transverse rows (from above down) 6–8 rows on tarsomere I of 0–1, 0–2, 2–4, 3–4, 3–6, 6–7, 6–8, and 6–7 teeth; tarsomere II with 5–6 rows of 0–2, 1–4, 4–6, 5–6, 5–7 and 4–6; and



Figures 26–37. Hypandria of *Drosophila ananassae* complex species. *Drosophila ananassae* (26) 1.5 km NW Taipivai, Nuku Hiva, Marquesas Islands; (27) Belvédère 250 m, fruit bait, Moorea, Society Islands, French Polynesia. *Drosophila ananassae* or *D. pallidosa* (28) Sigatoka, 35 km S Nadi, Fiji; (29) Apia, Samoa. *Drosophila pallidosa* (30) det. by ?Wheeler, Pago Pago, ... [continued on facing page]



Figures 38–53. Epandria of *Drosophila ananassae* complex species. *Drosophila pandora* sp.nov. (38) Lake Placid type strain CAQ408, lateral view; (39) type strain CAQ408, caudal view; (40) Lake Placid strain CAR274; (41) Lake Placid strain CAQ425. *Drosophila ananassae* (42) Beach Lane, Mauritius, Oct. 2012, J. Tann. *Drosophila ?ananassae* (43) Kuranda, northern Queensland, AMS K275429; (44) Sigatoka, 35 km S Nadi, Fiji, AMS K275290; (45) Iron Range, fruit bait, 30.iv.1976, I.R. Bock, [possibly pinned on this date from a strain collected with P.A. Parsons in November 1975—there is no evidence that Bock returned to Iron Range in 1976], AMS K119308 (det. *Drosophila ananassae* by Bock in 1976). *Drosophila pandora* sp.nov.: (46) *D. “papuensis-like”* Kyorin University stock k-aat001, Townsville, Queensland. *Drosophila pallidosa*: (47) det. by ?Wheeler, Pago Pago, American Samoa, Drosophila Species Stock Center (San Diego), stock 14024-0433.01. *Drosophila ananassae* or *D. pallidosa* (48) Sigatoka, 35 km S Nadi, Fiji, June 2004, Schug, Gray-Smith, Kilon-Attwood, McEvey, AMS K282851. *Drosophila schugi* sp.nov. (49) Malololelei, Upolu, Samoa, 14–17 June 2003, paratype AMS K282923. *Drosophila anomalata* sp.nov. (50–52) ex type strain, Schiffer CHC221. *Drosophila schugi* sp.nov. (53) Malololelei, Upolu, Samoa, 14–17 June 2003, AMS K356977. Localities—see Fig. 1 and Appendix 1; all specimens in Australian Museum.

Figures 26–37 [continued from facing page]. ... American Samoa, Drosophila Species Stock Center (San Diego), stock 14024-0433.01; (31) det. by ?Wheeler, Aopo, Savaii, Samoa, DSSC (San Diego), stock 14024-0433.00; (32) det. by ?Takanashi and/or ?Tobari (see Matsuda, 2014), Kyorin University stock k-aae002 from Lautoka, Fiji. *Drosophila ananassae* or *D. pallidosa* (33) Sigatoka, 35 km S Nadi, Fiji, June 2004, Schug, Gray-Smith, Kilon-Attwood, McEvey, AMS K282844. *Drosophila parapallidosa* (34) Kyorin University stock k-aas012, Kota Kinabalu, Malaysia. *Drosophila pandora* sp.nov. (35) *D. “papuensis-like”* [= *D. pandora* sp.nov.] Kyorin University stock k-aat001, Townsville, Queensland; (36) *D. “papuensis-like”* [= *D. pandora* sp.nov.] Kyorin University stock k-aat003, Wau, PNG. (37) *Drosophila pallidosa*-like-WAU, Kyorin University stock k-aav002, Bulolo (nr Wau), PNG. Localities—see Fig. 1 and Appendix 1; all specimens in Australian Museum.

Table 1. Number of rows in sex comb on male fore-tarsi of *Drosophila ananassae*, *D. anomalata* sp.nov. and *D. pandora* sp.nov.

species sample size leg	<i>D. ananassae</i> n = 99				<i>D. anomalata</i> sp.nov. n = 8				<i>D. pandora</i> sp.nov. n = 656			
	left		right		left		right		left		right	
	I	II	I	II	I	II	I	II	I	II	I	II
tarsomere (tarsal segment)												
number-range of sex comb rows	4–6	3–5	4–6	3–5	2–3	3	2	3	2–6	2–4	2–6	2–4
average number of sex comb rows	5	4	5	4	2	3	2	3	4	3	4	3

tarsomere III in 2 rows of 2–4 and 2–3 rows. Other thoracic measurements (holotype ♂)—pre-sc/pdc = 0.25, bsc/asc = 0.82, sterno-index = 0.61, m/a.kepst = 0.61, p.kepst/pdc = 1.12, pdc/asc = 0.81, asc–bsc/asc–asc = 1.19, a–pdc/dc-gap = 0.38, adc/pdc = 0.62, fw(a.oc)/dc-gap = 1.21.

Wing. Hyaline, wing length c. 1.9 mm. L(Ax) = 1.88 mm, WL = 1.71 mm, L₁ = 1.66 mm, L(Ax)/WW = 2.37, WL/WW = 2.16, L₁/WW = 2.10, C-index = 1.58, 4v-index = 2.60, 4c-index = 1.66, 5x-index = 2.48, M-index = 0.94, ac-index = 3.50, C3 fringe = 0.52.

Abdomen. Tergites dark especially posteriorly, apical tergites darker, tergite VI usually dark brown.

Male terminalia. *Epandrium* (*periphallic organs*) (Fig. 49) narrow dorsally and ventrally; toe elongate, with about 12 setae apically. Primary clasper (surstylus) and secondary clasper present. Surstylus large, with two sets of teeth—medial row of 4 strong pointed upper teeth and a cluster of about 8 lower pointed teeth (one greatly elongated, curved towards decastrum); and a lateral row of thicker, blunt, black, teeth in 2 sets: an upper of 2 (widely spaced) and a lower of 3–5 tightly spaced teeth. Secondary clasper small, with a very large curved black medial tooth, and about 3 small lateral setae.

Hypandrium (*phallic organs*). Aedeagus brown, non-bifid, narrowed in middle, and strongly hirsute in apical third (Figs 13, 68–71); aedeagal apodeme as long as the ventral phragma and considerably expanded in lateral view. Anterior parameres large, scimitar-shaped (Fig. 13) or with ragged lateral edge (Figs. 82–85), articulated to aedeagus, and laterally with no minute sensilla. Posterior parameres strongly tapering apically, long, extending past tip of aedeagus. Caudal margin of novasternum ill-defined, slightly hirsute, with no medial convexity, and with a pair of submedian spines not widely separated. Hypandrium with transverse band (example marked *tb* in Fig. 4) nearly as wide as ventral phragma.

Female. Unknown, difficult to identify except by extrapolation from male siblings or progeny.

Distribution. Known only from Upolu, Samoa: common at the type locality at Malololelei (c. 450 m), rare at Apia (sea-level).

Etymology. This species is named after Dr Malcolm D. Schug (University of North Carolina, Greensboro), who led two expeditions (with Shelly Gray Smith, Michael M. Marshall and Amanda Killon-Atwood) to northern Australia and islands of the South Pacific to explore genetic structure and historical demography of natural populations of *Drosophila ananassae*.

Remarks

In 1934 Malloch completed a taxonomic study of the Drosophilidae of Samoa, he reported on ten genera and 27 species, many of them he described as new. He discusses one species (species no. 20, p. 301) in context to *D. ananassae*. Specimens of this species, he notes, were available from the islands of Upolu, Savaii and Tutuila. On Upolu, Buxton and Hopkins had collected specimens at Apia (the capital of Samoa, at sea level) in August 1924 and at Malololelei (at c. 450 m) on 25 November 1924. When Malloch examined these flies he was confident they were all members of one species conspecific with *D. similis* that Lamb (1914) had described from the Seychelles. But the name *D. similis* was preoccupied in the genus *Drosophila* so Malloch proposed the replacement name *D. errans* Malloch. Malloch (1934a) also noted that *D. similis* [= *D. errans*] and *D. ananassae* were treated as synonyms by Duda. On this point he appears to have been unconvinced, and instead he emphasized his certainty that the species in Samoa was the same as the species in the Seychelles, leaving open the question of whether or not it was conspecific with *D. ananassae* from Ambon and elsewhere in southeast Asia. Malloch apparently did not dissect the male terminalia of any specimens, but he did describe the sex combs (Malloch, 1933): “The two basal segments of the fore tarsi in [males] have the ventral setulae arranged in transverse series that are quite conspicuous when seen transversely and as well figured by Lamb” (Lamb, 1914, plate XX, fig. 33; Malloch, 1933). The specimens in the USNM determined as *D. errans* by Malloch from Malololelei, should be re-examined—it is probable they are *D. schugi*. There is little doubt that *D. similis* Lamb is correctly synonymized with *D. ananassae* Doleschall (Cariou *et al.*, 2008) therefore we do not need to consider the possibility that the *similis*-replacement name *errans* may instead be the appropriate name for the species newly described here as *D. schugi*. Some or all of the Samoan specimens determined as *D. errans* by Malloch may indeed turn out to be *D. schugi* but this will have no substantive bearing on the taxonomy proposed here.

Harrison (1954) reported taking large numbers of *D. ananassae* from Upolu (Vailima and Malololelei), they too should be re-examined because we now know that three species of the complex exist on the island of Upolu: *D. ananassae*, *D. pallidosa* and *D. schugi*. Wheeler & Kamysellis (1966) also refer to “*D. ananassae*” specimens from Upolu noting that the pale and dark forms are probably different species—they were correct.

The genetic data presented by Schug *et al.* (2007, fig. 3) clearly shows that 23 of the 25 genotypes sampled at Apia and 11 genotypes derived from Malololelei flies are not drawn from the same population (i.e. the same species). There is evidence that 2 of the 25 genotypes from Apia are very closely related to the Malololelei genotypes. We

Table 2. Number of teeth in each row of the sex comb on the male fore-tarsi of *Drosophila ananassae*, *D. anomalata* sp.nov. and *D. pandora* sp.nov. showing bilateral variation or symmetry, total and average number of teeth per leg (cf. per tarsomere, Table 1). Numbering of rows begins at proximal end of tarsomere.

		<i>D. ananassae</i>		<i>D. anomalata</i> sp.nov.		<i>D. pandora</i> sp.nov.	
		no. of teeth per row		no. of teeth per row		no. of teeth per row	
		left	right	left	right	left	right
tarsomere I	1	0–2	0–2			0–1	0–1
	2	0–4	0–4			0–1	0–2
	3	1–6	1–5			0–3	0–3
	4	1–6	2–7	0–2		0–6	0–5
	5	4–9	4–8	1–3	1–3	2–8	2–8
	6	5–9	5–9	4–7	4–7	3–8	3–8
tarsomere II	1	0–2	0–1				
	2	0–4	0–3			0–2	0–2
	3	1–6	2–6	1–2	0–1	0–4	0–4
	4	3–6	3–6	2–4	2–4	2–6	1–5
	5	3–7	3–7	3–4	3–4	2–7	2–8
total number of teeth (range)		28–48	26–47	12–20	12–18	13–31	14–32
average number of teeth		37	37	15	14	22	22

conclude that *D. schugi* is more common at, but not restricted to, the higher elevation locality at Malololelei, it also occurs at low frequency (based on genetic evidence, ratio is 2:25) at sea level at Apia. The reverse is true: specimens that correspond to *D. pallidosa* (pale with low sex comb scores and *D. ananassae*-like male terminalia) are common at Apia and rare, but not absent, at Malololelei (among large numbers of specimens preserved in alcohol collected from Malololelei in 2003, we have detected some that have no sex combs on the third tarsal segment, a condition typical of *D. pallidosa* and *D. ananassae*, but because the specimens are pale we have determined them to be *D. pallidosa*).

Hybridization tests

A crossing experiment was designed to investigate hybrid fertility between *D. pandora*, *D. anomalata* and *D. ananassae*. *Drosophila pandora* and *D. ananassae* iso-female lines were derived from individuals collected at Lake Placid in 2011. *Drosophila anomalata* iso-female line CHC221 was collected near Deeragun in April 2014 and iso-female lines A5, A25, A29, A41 and A43 were collected from Lake Placid in November 2014.

Under laboratory conditions all pair-wise combinations of the three species—*D. ananassae*, *D. pandora* and *D. anomalata*—will mate. Of the nine possible pair-wise combinations all produce fertile F₁ progeny. However, the degree of F₁ fertility varies greatly. For example, of the three experiments, only one out of 60 crosses between *D. pandora* female and *D. ananassae* male produced fertile F₁ (Tables 3–5). In the reciprocal only 3 of the 60 yielded fertile F₁.

Drosophila ananassae and *D. anomalata* mate readily in both directions. Of the 320 single-pair crosses, in both directions, about 65% produce viable F₁. These first generation hybrids when inter-crossed with each other are nearly always fertile (Tables 3–5).

Drosophila pandora crossed with *D. anomalata* produces significantly fewer hybrids, about 30% of all hybridizations are viable and fertile.

The *D. ananassae* and *D. pandora* cross is the least successful, only about 10% are viable. Almost 100% sterility of F₁ hybrids occurs when *D. pandora* females are crossed with *D. ananassae* males. Conversely, in the reciprocal cross, on the rare occasion a hybrid is produced, it is always fertile.

Clearly these three species, which occur sympatrically in northern Queensland, warrant further study. The cause of the hybrid sterility is unknown, and an attempt has been made to address the complications that arise with *Wolbachia* infection by treating with tetracycline. The results in Table 4 demonstrate that *Wolbachia* has minimal impact and that cytoplasmic incompatibility is not responsible, in this case, for the observed sterility.

Male courtship behaviour

Working with live strains has allowed us to make some preliminary observations of courtship behaviour. Males of the three species *D. ananassae*, *D. pandora* and *D. anomalata* have distinctly different courtship behaviour. Most notably, bobbing behaviour of the *D. anomalata* male when in front of the female has been observed—a similar behaviour was described by Spieth (1966: 137) in his observation of strains from New Guinea and Queensland. We have been unable to locate specimens from those strains. Spieth also noted “striking differences in the wing displays of courting *D. pallidosa* and *D. ananassae*” (Spieth, 1966; Futch, 1973).

It was noticed during the rearing of *D. ananassae* and *D. pandora* that the third instar larvae behave differently just prior to pupation. While *D. ananassae* prefers to pupate on a piece of card placed in the rearing vial, or on the glass walls of the vial—particularly higher up, *D. pandora* third instar larvae tend to pupate only on the paper card. When a card is not provided, third instar *D. ananassae* larvae prefer to pupate above the surface of the culture medium, while third instar *D. pandora* larvae tend to remain below the surface of the culture medium with only the anterior spiracles exposed.

Table 3. Results of intra- and interspecific single-pair matings between *D. ananassae*, and the type strains of *D. pandora* sp.nov. and *D. anomalata* sp.nov. Virgin flies were sexed under CO₂ anaesthesia, isolated, and then allowed to recover for a minimum of 24 hours. There were 20 replicate vials for each parental cross. All vials were coded and randomized. Vials were regularly scored for presence of larvae, pupae and F₁ adults. When F₁ adults were present they were mated with each other to check for F₁ fertility and F₂ viability. Flies were maintained at 19.0 ± 1.0°C on a 12:12 light:dark cycle.

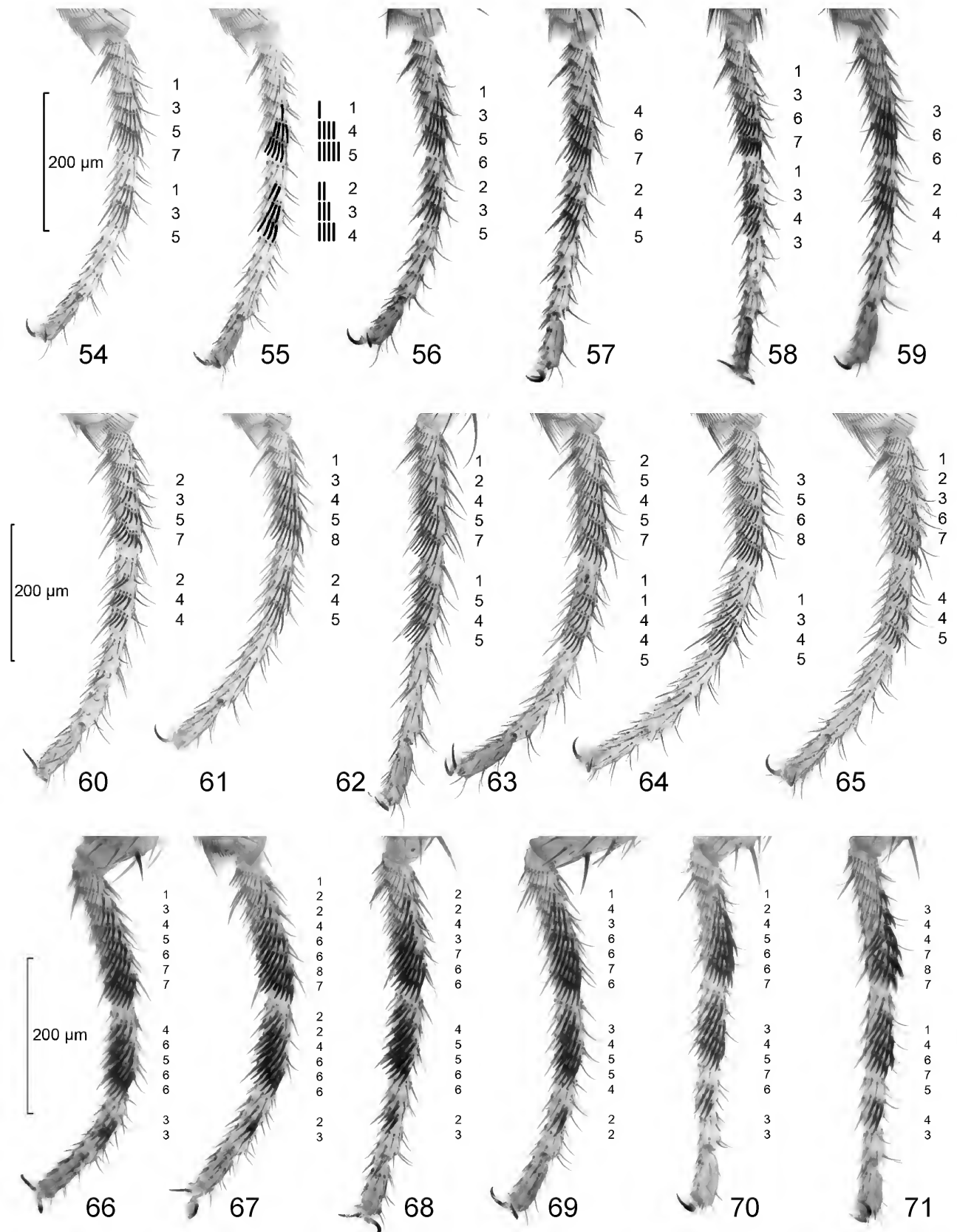
	<i>D. ananassae</i> (CBR57) ♂	<i>D. pandora</i> (CAQ408) ♂	<i>D. anomalata</i> (CHC221) ♂
<i>D. ananassae</i> (CBR57) ♀	19 F ₁ / 19 F ₂	0	13 F ₁ / 13 F ₂
<i>D. pandora</i> (CAQ408) ♀	3 F ₁ / 1 F ₂	20 F ₁ / 18 F ₂	11 F ₁ / 11 F ₂
<i>D. anomalata</i> (CHC221) ♀	16 F ₁ / 16 F ₂	6 F ₁ / 6 F ₂	19 F ₁ / 19 F ₂

Table 4. Results of intra- and interspecific single-pair matings between *D. ananassae* (CBR57), *D. pandora* (types strain CAQ408) and *D. anomalata* (type strain CHC221) with tetracycline (T) and without tetracycline treatment for *Wolbachia*. Virgin flies were sexed under CO₂ anaesthesia, isolated and then treated. See Table 3 for crossing protocol.

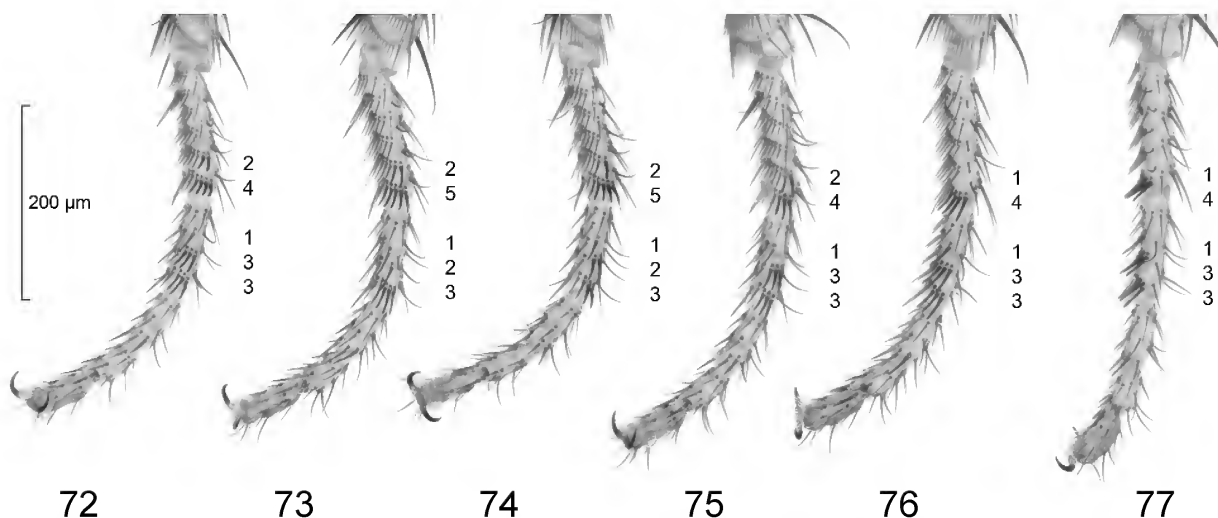
	<i>D. ananassae</i> ♂	<i>D. pandora</i> ♂	<i>D. anomalata</i> ♂	<i>D. ananassae</i> ♂ T	<i>D. pandora</i> ♂ T	<i>D. anomalata</i> ♂ T
<i>D. ananassae</i> ♀	14 F ₁ / 12 F ₂	1 F ₁ / 1 F ₂	4 F ₁ / 4 F ₂	—	—	—
<i>D. pandora</i> ♀	2 F ₁ / 0 F ₂	18 F ₁ / 17 F ₁	4 F ₁ / 4 F ₂	—	—	—
<i>D. anomalata</i> ♀	17 F ₁ / 16 F ₂	0	16 F ₁ / 15 F ₂	—	—	—
<i>D. ananassae</i> ♀ T	—	—	—	12 F ₁ / 11 F ₂	1 F ₁ / 1 F ₂	11 F ₁ / 11 F ₂
<i>D. pandora</i> ♀ T	—	—	—	3 F ₁ / 0 F ₂	18 F ₁ / 16 F ₂	1 F ₁ / 0 F ₂
<i>D. anomalata</i> ♀ T	—	—	—	13 F ₁ / 13 F ₂	4 F ₁ / 3 F ₂	18 F ₁ / 15 F ₂

Table 5. Results of intra- and interspecific single-pair matings between *D. ananassae*, and type strains of *D. pandora* sp.nov. and *D. anomalata* sp.nov., and five additional iso-female lines of *D. anomalata* sp.nov. from Lake Placid (A5, A25, A29, A41 and A43). See Table 3 for crossing protocol.

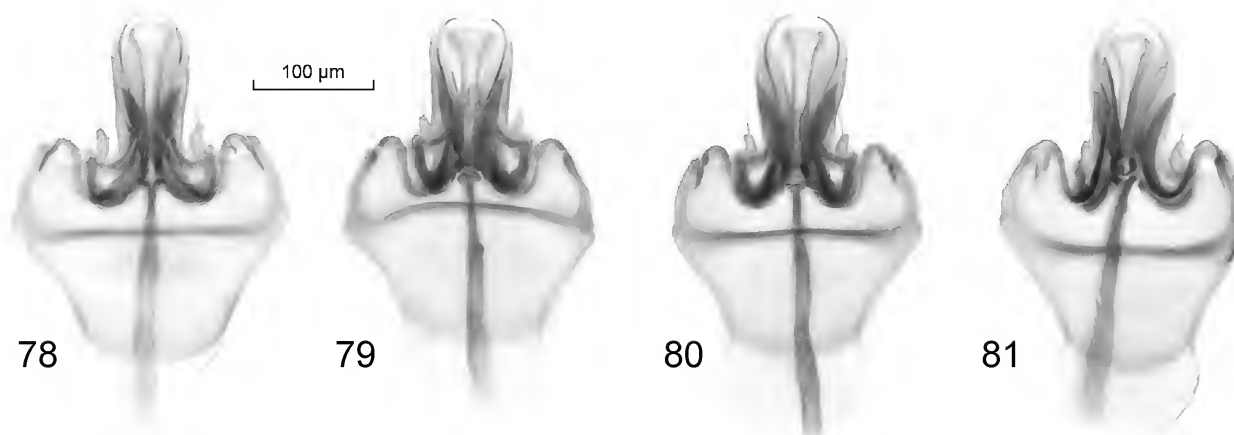
	<i>D. ananassae</i> ♂	<i>D. pandora</i> ♂	<i>D. anomalata</i> ♂	<i>D. anomalata</i> A5 ♂	<i>D. anomalata</i> A25 ♂	<i>D. anomalata</i> A29 ♂	<i>D. anomalata</i> A41 ♂	<i>D. anomalata</i> A43 ♂
<i>D. ananassae</i> ♀	16 F ₁ / 16 F ₂	1 F ₁ / 1 F ₂	14 F ₁ / 14 F ₂	17 F ₁ / 17 F ₂	12 F ₁ / 12 F ₂	13 F ₁ / 13 F ₂	14 F ₁ / 14 F ₂	17 F ₁ / 16 F ₂
<i>D. pandora</i> ♀	3 F ₁ / 0 F ₂	17 F ₁ / 17 F ₂	3 F ₁ / 3 F ₂	7 F ₁ / 6 F ₂	4 F ₁ / 4 F ₂	6 F ₁ / 6 F ₂	11 F ₁ / 11 F ₂	5 F ₁ / 5 F ₂
<i>D. anomalata</i> ♀	17 F ₁ / 17 F ₂	10 F ₁ / 10 F ₂	16 F ₁ / 15 F ₂	16 F ₁ / 16 F ₂	17 F ₁ / 16 F ₂	19 F ₁ / 18 F ₂	19 F ₁ / 19 F ₂	20 F ₁ / 20 F ₂
<i>D. anomalata</i> A5 ♀	14 F ₁ / 14 F ₂	2 F ₁ / 2 F ₂	20 F ₁ / 20 F ₂	19 F ₁ / 19 F ₂	—	—	—	—
<i>D. anomalata</i> A25 ♀	15 F ₁ / 15 F ₂	9 F ₁ / 9 F ₂	19 F ₁ / 19 F ₂	—	17 F ₁ / 16 F ₂	—	—	—
<i>D. anomalata</i> A29 ♀	17 F ₁ / 17 F ₂	5 F ₁ / 5 F ₂	19 F ₁ / 19 F ₂	—	—	19 F ₁ / 19 F ₂	—	—
<i>D. anomalata</i> A41 ♀	14 F ₁ / 14 F ₂	8 F ₁ / 8 F ₂	20 F ₁ / 20 F ₂	—	—	—	19 F ₁ / 19 F ₂	—
<i>D. anomalata</i> A43 ♀	7 F ₁ / 7 F ₂	8 F ₁ / 8 F ₂	17 F ₁ / 17 F ₂	—	—	—	—	17 F ₁ / 17 F ₂



Figures 54–71. Male fore-leg and sex comb of tarsomere I (metatarsus or basitarsus), tarsomere II and III of *Drosophila pandora* sp.nov. (54–59), *D. ananassae* (60–65) (from strains established by Schiffer at Lake Placid, northern Queensland) and *D. schugi* sp.nov. (66–71). *Drosophila pandora* sp.nov. (54–55) from iso-♀ strain CAR274 [the teeth of the sex comb in Fig. 51 are artificially enhanced and represented schematically to indicate how they are scored]; (56–57) from type strain = iso-♀ strain CAQ408; and (58–59) from iso-♀ strain CAQ425. *Drosophila ananassae* (60–61) from iso-♀ strain CBR57; (62–63) from iso-♀ strain CBR54; and (64–65) from iso-♀ strain CBR52. *Drosophila schugi* sp.nov. wild caught males from Malololelei, Upolu, Samoa, 14–17 June 2003, Schug, Gray-Smith, Kilon-Attwood, McEvey; AMS K356978 (66), AMS K356979 (67–68), AMS K356977 (69), and AMS K356976 (70–71).



Figures 72–77. Male fore-leg and sex comb of tarsomere I (metatarsus) and II of *Drosophila anomalata* sp.nov. ex type strain CHC221, nr Deeragun, 16 km W of Townsville. Legs from five males; (73–74) left and right legs from one male [(74) image flipped].



Figures 78–81. Hypandria of *Drosophila anomalata* sp.nov. three males from the type strain Schiffer CHC221 (ventral views); (81) dorsal view of hypandrium in Fig. 80.



Figures 82–85. Hypandria of *Drosophila schugi* sp.nov. four males collected with holotype at Malalololei, Upolu, Samoa, 14–17 June 2003, Schug, Gray-Smith, Kilon-Attwood, McEvey; AMS K356976 (82), AMS K356977 (83), AMS K356978 (84), AMS K356979 (85).

Discussion

Habitat preference. A range of drosophilids are attracted to fruit baits in northern Australia and New Guinea. Species of *Drosophila* s.st., *Drosophila* (*Sophophora*) and *Scaptodrosophila* are the most common. Within the *melanogaster* species group of *Sophophora*, species of the *ananassae*, *montium* and *melanogaster* species subgroups are particularly abundant on fermenting fruit and are part of the fauna associated with fruit-decay in Australo-Papuan rainforests. While species of the *ananassae* subgroup are always a large proportion of the drosophilid fauna on rotting fruit in the Australian tropics, the ratio of *D. pandora*, *D. ananassae* and *D. anomalata* varies considerably in any one sample. The variation is apparently dependent upon habitat type and humidity levels during the weeks prior to collection. For example, at a peridomestic garden habitat at Lake Placid, the ratio of the three species was *D. ananassae*: *D. anomalata*: *D. pandora* = 13:0:33 in April 2014 (wet season) and 29:5:10 in November 2014 (dry season). In an adjacent less-disturbed rainforest habitat, also in November 2014, the ratio was 1:1:4.

Bock and Parsons collected at Bamaga and Iron Range in northern Queensland in November 1975 at the end of the dry season. At Iron Range they took only 29 specimens at fruit bait. But the diversity was high: six *Sophophora* species were present among the 29 specimens, the most common (62%) was determined by Bock to be *D. ananassae* and *D. ironensis* was 24% of the catch.

Male sex comb morphology. *Drosophila pallidosa*, *D. anomalata* and *D. ananassae* are perhaps the most difficult species to distinguish in the *ananassae* complex. Bock & Wheeler (1972) suggest that, apart from the difference in abdominal pigmentation in Samoan specimens [of *D. ananassae* and *D. pallidosa*], the single morphological difference is “the reduced number of rows of the sex comb of *D. pallidosa* in comparison with *D. ananassae*”.

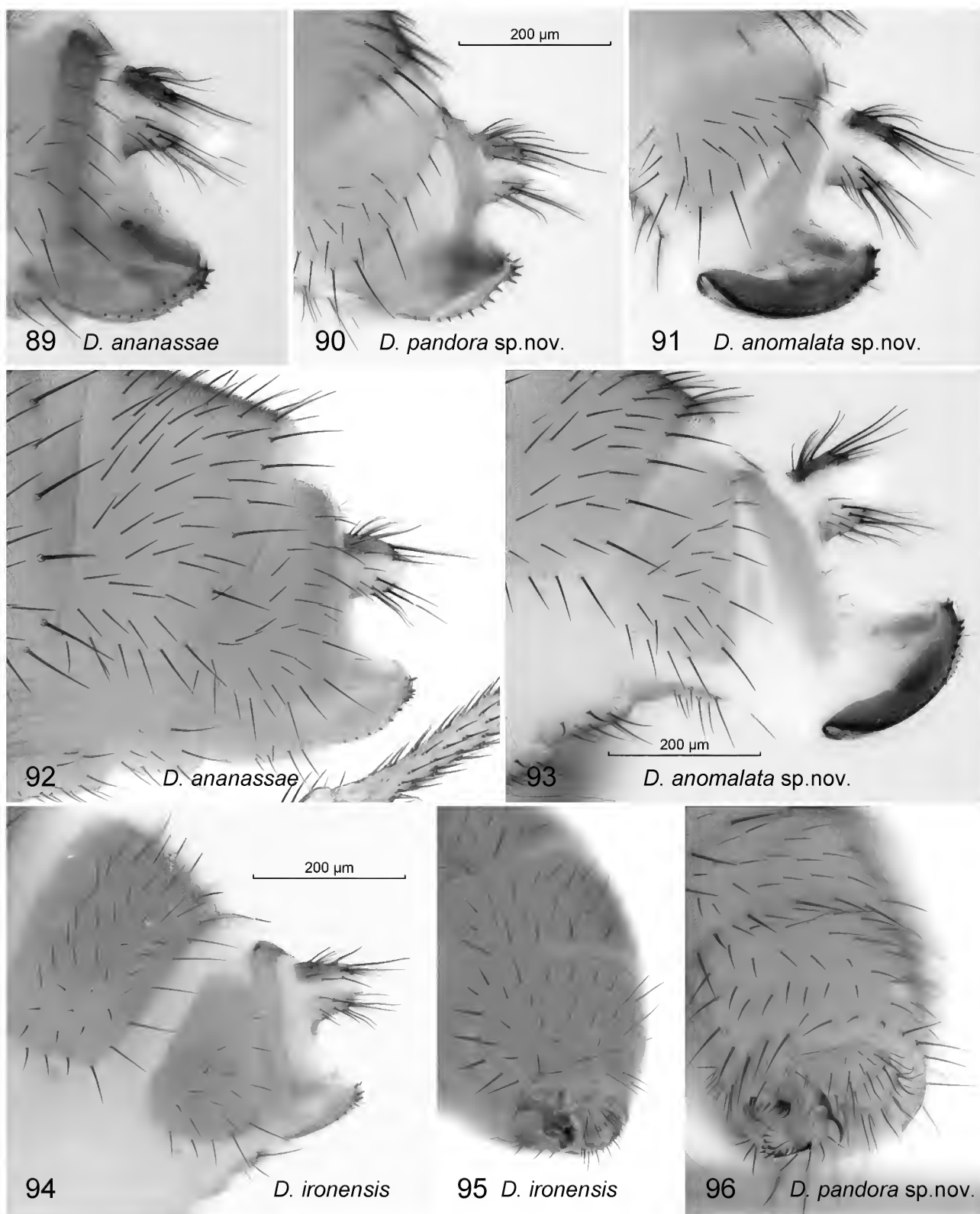
Examination of the male terminalia is a useful diagnostic for distinguishing *D. pandora* from the other members of the complex but not for differentiating *D. anomalata*, *D. ananassae* and *D. pallidosa* (sensu Bock & Wheeler, 1972); the latter three are apparently indistinguishable on terminalia alone. A comprehensive study of male sex comb morphology has, however, yielded important diagnostic parameters that do separate *D. anomalata* and *D. ananassae*. Since we have been unable to examine *D. pallidosa* type material, we can only guess that our pale Fijian and Samoan specimens with a reduced number of rows of the sex comb are *D. pallidosa* (data not shown).

Ninety-nine *D. ananassae* field-collected Australian specimens (see Tables 1 and 2) were examined to determine sex comb number and arrangement. Eight *D. anomalata* males representing offspring from four iso-female lines and 656 *D. pandora* field-collected males from localities between Rockhampton and Cooktown (Table 1, Fig. 1) were examined to determine sex comb number and arrangement. The results are presented here in two tables. Table 1 shows that there is a large and overlapping variation in the *number of rows* per leg making this particular metric a poor diagnostic for separating these species.

McEvey *et al.* (1987) showed that scoring the total number of teeth in the combs rather than the actual number of rows led to greater discrimination between taxa. Tables 1 and 2



Figures 86–88. *Drosophila schugi* sp.nov. holotype AMS K282922. Dorsal, lateral and anterolateral views of the head and face.



Figures 89–91. Female oviposcept (ovipositor) and setation of sixth abdominal tergite of *Drosophila ananassae*, *D. pandora*, *D. anomalata* and *D. ironensis*. Oviscept form and colour: (89) *Drosophila ananassae* ex strain Schiffer CBR57 from Lake Placid; (90) *D. pandora* sp.nov. ex type strain Schiffer CAQ408 from Lake Placid; (91) *D. anomalata* sp.nov. ex type strain Schiffer CHC221 from near Deeragun, W of Townsville. Setation of sixth abdominal tergite: (92) *D. ananassae* ex strain Schiffer CBR54; (93) *D. anomalata* sp.nov. ex type strain; (94, 95) *Drosophila ironensis* ♀ and ♂ ex strain Schiffer CHH18 from Lake Placid, note the irregular orientation of T6 setation in *D. ironensis* compared to the caudally oriented setation in other figured species; and (96) *D. pandora* sp.nov. ♂ ex type strain. All to same scale.

show the results of scoring of teeth-number per comb and teeth number per leg. In most instances teeth-number per leg enables differentiation of the three species. *Drosophila ananassae* has 29–48 teeth per leg, *pandora* has 13–32 and *anomalata* has 12–20. Only on those rare instances when teeth-number falls in the overlapping range is examination of the terminalia required. With experience this can be done on live or dead males without dissection because the convexity of the novasternum protrudes and is often visible with good microscopy.

Biogeography—the Sahul Shelf and the isolation of the Darwin fauna. Numerous drosophilid species that were first discovered in northern Australia have now been found in New Guinea (Carson & Okada, 1982; McEvey, unpublished); many other insects have ranges that are continuous across large parts of New Guinea and into Australia (Taylor, 1972). Northern Queensland has the richest drosophilid fauna of anywhere in Australia. It has become evident (McEvey & Bock, 1982), however, that the fauna of northern Queensland is but a fraction of the hugely diverse fauna of New Guinea (Okada, 1970). Despite the diversity in New Guinea only about 28 drosophilid species were reported from all of New Guinea before 1955; *Drosophila ananassae* was not one of these. In 1955 no drosophilid species were reported from Darwin, and none from Cape York Peninsula, except *Acletoxenus quadristriatus* Duda, 1936 from Thursday Island.

The continuity or connectedness between the fauna of southern New Guinea (New Guinea south of the Central Range) and northern Australia becomes evident in light of studies of sea level fluctuations of the shallow Torres Strait that currently covers the *Sahul Shelf*. Sahul is the Pleistocene Era land mass that connects New Guinea, Australia and Tasmania. On a continental scale Sahul abuts Sunda (Sunda is most of southeast Asia west of New Guinea, Fig. 1). During the last 200,000 years New Guinea and northern Queensland rainforests have been continuous for some 180,000 years (Williams, 2001). Torres Strait has divided New Guinea and Australia for only two relatively short periods: once about 120,000 years ago and a second short period more recently from about 8,000 years ago to the present. These two short interruptions during the last 200,000 years represent important barriers to gene flow between populations of drosophilid species adapted to lowland habitats of the region. With higher sea-levels during the last 8,000 years, drosophilid populations of Cape York Peninsula rainforests (and to a lesser extent those rainforests in Arnhem Land, Northern Territory) have become isolated in “rainforest refugia” and are best understood as residual subsets of larger more diverse complexes of species existing in New Guinea. During Pleistocene periods of lower relative sea levels, the Sahul Shelf between New Guinea and northern Australia was exposed subaerially and the Australian mainland was broadly “joined” by land and rainforest to New Guinea (Williams, 2001; Collier, 2007). At the same time, summer rainfall exceeded 400 mm across a broad swathe of northern and eastern Australia (Williams, 2001).

Rainforest habitats extending from southern New Guinea to northern Australia, expand and contract depending on long term climate, fire and sea-level patterns (Collier, 2007). In recent times climate and fire have favoured the retraction of rainforest areas of northern Australia into discrete “islands” (Stanton, 1976). Large, but isolated, rainforests occur on Moa

island (Torres Strait), at Bamaga, Heathlands, in the Iron, McIlwraith and Melville Ranges, then in the mountains and foot hills of the Great Dividing Range from Cape Tribulation to Townsville. Despite the numerous xeric barriers that now exist, e.g., *The Carpentarian Gap* and *The Ord Arid Intrusion* (Bowman *et al.*, 2010), no evidence of speciation has been found among these isolated rainforests, except that the “dominance” of the New Guinean drosophilid fauna diminishes southwards (McEvey, 1994). Rainforests of New Guinea cover most of the island, whereas rainforests of Australia extend like an archipelago of islands down the eastern mountain chain—The Great Dividing Range. Each “island” of rainforest is isolated by xeric sclerophyllous scrub and open woodlands. Large isolated rainforests are tenuously connected by veins of intermittent riparian forest that provide desiccation relief during the dry season (McEvey, 1993).

The rainforests of Queensland above 16° latitude (Fig. 1) are difficult to access especially during the wet season (January–May), when conditions are best for collecting. It is, therefore, not surprising that knowledge of the drosophilid fauna of Cape York Peninsula derives only from the following expeditions.

Iron Range 1966 McAlpine, Holloway
 Iron Range 1971–1972 McAlpine, Holloway
 Iron Range 1975 Bock, Parsons
 Iron Range 1976 Bock
 Torres Strait 1979–1980 McEvey
 Iron Range 1981 McEvey
 Cooktown 1980–1981 Colless
 Heathlands 1992 Daniels, Schneider, McEvey
 Iron Range 2002 Schiffer
 Torres Strait 2003 Schug, Gray-Smith, Marshall, McEvey
 McIlwraith Range 2004 McEvey
 Iron Range 2006 van Klinken
 Iron Range–Bamaga 2007 Schiffer, Mitrovski
 Iron Range 2013 Schiffer, Blackhall

There have been numerous other entomological surveys of Cape York Peninsula. For example, the CSIRO ANIC expeditions, and especially the extensive CYPLUS surveys with long-term Malaise trapping across many locations. But these have not yielded additional information on Drosophilidae, the drosophilids in Malaise-trap “soups” remain unprocessed and unknown. Whereas from Cairns southwards the number of surveys that have targeted *Drosophila* species is much higher—the intensity of “collecting effort” much greater. Biogeographic interpretation based on museum or literature records needs to take account of this uneven distribution of “collecting effort” throughout northeastern Australia.

The distribution and relative abundance of *D. ananassae*, *D. pandora* and *D. anomalata* in northern Australia and New Guinea is uncertain because the three species were conflated prior to this study. Mather (1955) found “*D. ananassae*” to be common near Cairns (Tolga, Babinda, Tully) and on Thursday Island. But Bock & Wheeler (1972) disagreed, suspecting incorrect identification. Instead they regarded the species as uncommon, citing just two records. During the following years Bock (1976) and Bock & Parsons (1978) found nothing to change this view, *D. ananassae* continued to be viewed as a species that “occasionally occurs in north Queensland rain forests”. The Bock and Parson collecting trip to Bamaga and Iron Range (Fig. 1) had taken place in early November 1975 during the dry season. At Iron Range they collected only 29 specimens at fruit bait—six species of

the subgenus *Sophophora*, comprising 18 (62%) specimens of “*D. ananassae*”, and 7 (24%) of *D. ironensis*. We are unable to explain why *D. pandora* was not discovered on this occasion, except that perhaps it was in fact collected, but assumed to be *D. ananassae* and therefore not treated as worth maintaining as a live culture (these specimens cannot now be located for confirmation). McEvey’s wet season expeditions to Torres Strait islands (1979–1980) and Iron Range (1981) found *D. pandora* (det. *D. ananassae* by McEvey and by Bock in 1981) to be very common on the islands and uncommon at Iron Range (McEvey, 1982; McEvey & Bock, 1982). The work of Schug *et al.* (2007) was based on this understanding and *D. pandora* was mistaken for *D. ananassae* in most instances. Instead the present

comprehensive study of male terminalia across the entire region has shown that most of the specimens collected at Iron Range and in Torres Strait were *D. pandora* and not *D. ananassae*.

Rieks van Klinken (2002) detected a species close to *D. ananassae* at very high frequency at fruit baits in small rainforest refugia near Darwin, Northern Territory. In pers. comm. to McEvey, van Klinken observed that sex comb development was so weak in males that they seemed to him to more closely resemble the inornate *D. ironensis* rather than the more lavishly adorned *D. ananassae*. Recent collecting by us (see under *Specimens examined*) yielded very high frequency of *D. pandora* at Holmes Jungle, near Darwin (no *D. ananassae* and no *D. ironensis* were found).

Key to *ananassae* subgroup species of Australia and New Guinea

The *Drosophila ananassae* subgroup flies, in Australia and New Guinea, are small (2–3 mm) pale yellowish-tan flies that frequently swarm over fermenting fruit, especially at latitudes lower than 20°S (Fig. 1), at altitudes below 1000 m (Appendix 1), and near or in dense humid forests. They will enter buildings and kitchens, disturbed habitats and gardens; they are, for example, common in suburban Cairns, Port Moresby, Darwin and Townsville. The abdomens are weakly banded or un-banded (e.g., Figs. 92–96) in both sexes. Only in *D. parabipectinata* Bock, 1971 (Christmas Island) and in the dark phenotype of *D. ananassae* (Norfolk Island and other South Pacific islands) are the apical abdominal segments dark or blackened (oviscapt pigmentation unknown*). Females are exceedingly difficult to separate in most species. Males can be sorted in an approximate fashion by reference to the sex combs on their fore-tarsi; but confident determination, of dead material, is possible only by dissection or direct observation of male terminalia. Even then, some species remain extremely difficult to identify (e.g., *D. ananassae*, *D. pallidosa* and *D. anomalata*). But all species are readily cultured in the lab and this opens the possibility for detailed study of sexual behaviour, genotype, karyotype, and other aspects of biology.

- | | | |
|---|--|--|
| 1 | Male | 2 |
| — | Female | 6 |
| 2 | Tarsomere I of foreleg with sex combs and last abdominal tergite with setae pointing caudally (e.g., Fig. 96) | 3 |
| — | Tarsomere I of foreleg with no sex comb and last abdominal tergite with setae pointing in all directions (e.g., Fig. 95) | <i>D. ironensis</i> |
| 3 | Sex combs consisting of two strong and oblique rows of teeth on tarsomere I and a single tooth or two teeth on tarsomere II distally | <i>D. bipectinata</i> |
| — | Sex comb of male consisting of transverse rows of bristles on tarsomere I and II | 4 |
| 4 | Sex comb consisting of 2 rows of bristles on tarsomere I and 1 row on tarsomere II | <i>D. pseudoananassae</i> |
| — | Sex comb consisting of 2–6 rows of bristles on tarsomere I and 2–5 rows on tarsomere II | 5 |
| 5 | Total number of tarsal teeth 29–48 (average 37), medial convexity of novasternum as in Figs. 60–65 | <i>D. ananassae</i> |
| — | Total number of teeth 13–32 (average 22), medial convexity of novasternum in the shape of a viking helmet, as in Figs. 54–59 | <i>D. pandora</i> sp.nov. |
| — | Total number of teeth 12–20 (average 14), medial convexity of novasternum as in <i>D. ananassae</i> , as in Figs. 72–77 | <i>D. anomalata</i> sp.nov. |
| 6 | Last abdominal tergite with setae pointing in all directions (Fig. 94) | <i>D. ironensis</i> |
| — | Last abdominal tergite with setae pointing caudally (Figs. 92–93) | 7 |
| 7 | Oviscapt darkly pigmented (Figs. 91, 93) * | <i>D. anomalata</i> |
| — | Oviscapt pale (e.g., Figs. 89–90, 92) | <i>D. ananassae</i> , <i>D. pandora</i> ,
<i>D. pseudoananassae</i> , <i>D. bipectinata</i> |

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Appendix 1. Distributional data for *Drosophila ananassae* subgroup species, arranged by longitude starting in Africa, ending in the eastern Pacific. Geo-spatial precision is approximately indicated by number of decimal places (map datum WGS84). This list is an attempt to summarize all published data (see text), and the authors (SMcE and MS) unpublished collection records for Australia, New Guinea and the Pacific south of the Equator. Altitudinal data is indicative only. The *locality* field is an informal placename based on label-data and used for databasing. *Drosophila imparata* Walker, 1859 is regarded as a synonym of *D. ananassae* from Aru Island (−6° 135°, between Darwin and New Guinea, see Fig. 1), types are lost. *Drosophila* “papuensis-like” is a synonym of *D. pandora* sp.nov., localities for “papuensis-like” are from Matsuda *et al.*, 2009. We have not examined specimens det. *D. pallidula* from Noumea, New Caledonia (Matsuda *et al.*, 2009). Undissected and equivocal records are listed as *ananassae* subgroup.

locality	country	latitude	longitude	altitude	<i>D. ananassae</i>	<i>D. atripex</i>	<i>D. imparata</i>	<i>D. lachaisei</i>	<i>D. monieri</i>	<i>D. ochrogaster</i>	<i>D. phaeopleura</i>	<i>D. pallidosa</i>	<i>D. pandora</i> sp. nov.	<i>D. anomalata</i> sp. nov.	<i>D. schugi</i> sp. nov.	<i>pallidosa</i> -like	"papuensis"-like	<i>ananassae</i> subgroup	<i>pallidosa</i> -like Wau	<i>pallidosa</i> 3038.1	<i>ananassae</i> 3038.2
Taï	Ivory Coast	8.17°	-7.53°		-	-	-	■	-	-	-	-	-	-	-	-	-	-	-	-	-
Lulumbashi (Elisabethville)	Congo-Kinshasa	-0.92°	15.17°		-	-	-	■	-	-	-	-	-	-	-	-	-	-	-	-	-
Mbuluzi Nature Reserve	Swaziland	-26.1373°	32.0093°	150–160m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranomafana	Madagascar	-21.25°	47.45°	950–1000m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mandraka	Madagascar	-18.911°	47.895°	1350–1390m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Andasibe	Madagascar	-18.932°	48.425°	920–1000m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maroantsetra	Madagascar	-15.43°	49.73°	5–20m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gratte Fesse	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
La Veuve Reserve	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mahé, Jardin Botanique	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mare aux Cochons dist., Mahé	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Mount Corgat	Seychelles	-4°	55°	400m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Seychelles	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vallée de Mai	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Victoria marché	Seychelles	-4°	55°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Réunion	Réunion	-21.2°	55.5°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morcellement Jhuboo	Mauritius	-20.036°	57.548°	5–15m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grand Baie	Mauritius	-20.02°	57.58°	5m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Beach Lane	Mauritius	-19.995°	57.593°	5–10m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mauritius	Mauritius	-20.3°	57.6°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
La Nicolière	Mauritius	-20.16°	57.61°	330–340m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
La Nicolière 337m	Mauritius	-20.1646°	57.6250°	335–340m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saint Antoine	Mauritius	-20.037°	57.651°	15m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mahébourg	Mauritius	-20.412°	57.707°	3m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
West Island	Australia	-12.174°	96.820°	1–5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Home Island	Australia	-12.0906°	96.8847°	1–5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Pak Chong	Thailand	14.72°	101.38°		-	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bogor Botanical Gardens	Indonesia	-6.599°	106.800°	250–270m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Jakarta	Indonesia	-6.17°	106.83°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malang	Indonesia	-7.97°	112.64°	430–490m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mumbul Inn Ubud	Indonesia	-8.5057°	115.2608°	225–230m	■	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ujung Pandang	Indonesia	-5.143°	119.429°	5–20m	■	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bantimurung	Indonesia	-5.0172°	119.6816°	80–90m	■	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Taiwan	Taiwan	23°	121°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KRIP site M21/2E2	Australia	-16.3604°	124.7684°		-	-	-	-	-	-	-	-	■	-	-	-	-	-	-	-	-
Maluku	Indonesia	-3°	128°		■	-	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sawinggrai	Indonesia	-0.535°	130.584°	1–5m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alawa	Australia	-12.3783°	130.8785°	22–23m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Casuarina Cubillo Street	Australia	-12.3730°	130.8863°	30–35m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Darwin	Australia	-12.4°	130.9°	4–50m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Karama	Australia	-12.403°	130.918°	35–40m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Berrimah Research Station	Australia	-12.434°	130.926°	40m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Holmes Jungle	Australia	-12.3978°	130.9345°	15–20m	■	-	-	-	-	-	-	-	■	-	-	-	-	-	-	-	-
Adelaide River	Australia	-13.240°	131.108°	55–60m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Wildman River	Australia	-12.83°	131.95°	10–40m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kakadu	Australia	-12.8°	132.8°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabar Miokre	Indonesia	-0.707°	135.601°	25–40m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Tabubil 470 m (riparian)	Papua New Guinea	-5.261°	141.218°	460–650m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Tabubil 570 m (OTML Env.)	Papua New Guinea	-5.2584°	141.2202°	560–580m	■	-	-	-	-	-	-	-	■	-	-	-	-	-	-	-	-
Tabubil 502 m (Donga)	Papua New Guinea	-5.2731°	141.2281°	490–510m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Tabubil 365 m (Six-Mile)	Papua New Guinea	-5.3065°	141.2508°	360–370m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-

Appendix 1 (continued).

locality	country	latitude	longitude	altitude	<i>D. ananassae</i>	<i>D. atripex</i>	<i>D. imparata</i>	<i>D. lachaisei</i>	<i>D. monieri</i>	<i>D. ochrogaster</i>	<i>D. phaeopleura</i>	<i>D. pallidosa</i>	<i>D. pandora</i> sp. nov.	<i>D. anomalata</i> sp. nov.	<i>D. schugi</i> sp. nov.	<i>pallidosa</i> -like	"papuensis"-like	<i>ananassae</i> subgroup	<i>pallidosa</i> -like Wau	<i>pallidosa</i> 3038.1	<i>ananassae</i> 3038.2
Mabuiag	Australia	-9.952°	142.183°	10–130m	–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Thursday Island (backyard)	Australia	-10.583°	142.217°	10–25m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Thursday Island	Australia	-10.58°	142.22°	0–60m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Moa (Aristolochia creek ford)	Australia	-10.1586°	142.3234°	20–30m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Moa (turkey mounds)	Australia	-10.163°	142.325°	20m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Moa (mango tree creek)	Australia	-10.170°	142.332°	10–20m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Moa (St Pauls Mission)	Australia	-10.188°	142.334°	1–10m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Gunshot Creek	Australia	-11.7193°	142.4811°	65–70m	–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Heathlands HS	Australia	-11.7507°	142.5818°	110–115m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Bertie Creek Pump	Australia	-11.7568°	142.5905°	88–90m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Mt Adolphus Island (rainforest)	Australia	-10.633°	142.658°	120–150m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Doublemouth Creek	Australia	-11.617°	142.816°	50–60m	–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Kuminibus	Papua New Guinea	-3.631°	143.031°	200–210m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Bainyik	Papua New Guinea	-3.662°	143.050°	145m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Iron Range	Australia	-12.71°	143.29°	20–100m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Gordon Creek	Australia	-12.7130°	143.2986°	47–50m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Mt Webb 3NE	Australia	-14.937°	145.119°	30–40m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Cooktown Caravan Park	Australia	-15.4769°	145.2439°		–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Mt Cook forest remnant	Australia	-15.4836°	145.2561°		–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Mossman 5W	Australia	-16.473°	145.331°	100–110m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Meelele Creek	Australia	-15.970°	145.395°	190–205m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Goroka	Papua New Guinea	-6.1°	145.4°	1600m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Daintree Icecream	Australia	-16.2131°	145.4047°		–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Lync Haven retreat	Australia	-16.2019°	145.4097°		–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Canopy Crane Facility forest	Australia	-16.103°	145.448°	60–70m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Canopy Crane Facility pig trap	Australia	-16.1042°	145.4550°	20m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Coconut Beach	Australia	-16.114°	145.456°	5–10m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Cape Trib Farmstay	Australia	-16.0858°	145.4608°		–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Grey's fruit farm	Australia	-16.0848°	145.4630°	10–20m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Tolga	Australia	-17.224°	145.479°	750–770m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Lake Eacham	Australia	-17.2795°	145.6269°	785–790m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Lake Barrine	Australia	-17.2575°	145.6322°	790–810m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Kuranda garden	Australia	-16.8137°	145.6433°	360–370m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Tully River	Australia	-17.78°	145.66°	60–300m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Smiths Track Trailhead	Australia	-16.8763°	145.6688°	90–100m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Lake Placid, rainforest remnant	Australia	-16.8676°	145.6733°		■	–	–	–	–	–	–	■	■	–	–	–	–	–	–	–	–
Lake Placid	Australia	-16.868°	145.674°	20–40m	–	–	–	–	–	–	–	■	–	■	–	–	–	–	–	–	–
Lake Placid tourist park	Australia	-16.8714°	145.6744°	16m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Manus Trinity Beach	Australia	-16.7963°	145.6925°	10–15m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Redlynch	Australia	-16.88°	145.70°		■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Maple Creek	Australia	-17.6706°	145.7239°	650–670m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Gordonvale 13SW	Australia	-17.182°	145.724°	60–65m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Cairns	Australia	-16.92°	145.75°	0–25m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Mulgrave River	Australia	-17.212°	145.751°	100–140m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Gordonvale 14S	Australia	-17.222°	145.761°	210–220m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Mulgrave River, 220m	Australia	-17.2212°	145.7620°	220m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Cairns	Australia	-16.9°	145.8°	0–5m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Cairns CBD	Australia	-16.921°	145.775°	0–5m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Gordonvale 18S	Australia	-17.256°	145.781°	125–130m	■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Mt Tyson	Australia	-17.93°	145.92°	30m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Tully	Australia	-17.935°	145.932°	15–20m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Innisfail, Dillon Rd	Australia	-17.4964°	145.9942°		■	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Innisfail Mango Tree Pk	Australia	-17.5456°	146.0286°		–	–	–	–	–	–	–	■	–	■	–	–	–	■	–	–	–
Dunk Island	Australia	-17.935°	146.144°	15–25m	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–	–
Palm Island	Australia	-18.733°	146.583°		■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–

Appendix 1 (continued).

locality	country	latitude	longitude	altitude	<i>D. ananassae</i>	<i>D. atripex</i>	<i>D. imparata</i>	<i>D. lachaisei</i>	<i>D. monteri</i>	<i>D. ochrogaster</i>	<i>D. phaeopleura</i>	<i>D. pallidosa</i>	<i>D. pandora</i> sp.nov.	<i>D. anomalata</i> sp.nov.	<i>D. schugi</i> sp.nov.	<i>pallidosa</i> -like	"papuensis"-like	<i>ananassae</i> subgroup	<i>pallidosa</i> -like Wau	<i>pallidosa</i> 3038.1	<i>ananassae</i> 3038.2
Vivian Voss Court	Australia	-19.237°	146.611°	22–22m	–	–	–	–	–	–	–	–	■	–	–	–	–	■	–	–	–
Headshump Forest	Papua New Guinea	-7.169°	146.620°	800–900m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bulolo	Papua New Guinea	-7.19°	146.65°		■	–	–	–	–	–	–	–	–	–	–	■	–	–	–	■	–
Deeragun garden	Australia	-19.2410°	146.6644°	16–17m	■	–	–	–	–	–	–	–	■	■	–	–	–	–	–	–	–
Townsville 17SW	Australia	-19.3758°	146.7050°	25–30m	■	–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–
Mt Kaindi 1200m	Papua New Guinea	-7.343°	146.707°	1200m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Wau	Papua New Guinea	-7.33°	146.72°	1150m	■	–	–	–	–	–	–	–	■	–	–	■	■	–	■	–	–
Aroana Estate	Papua New Guinea	-8.95°	146.91°	30–100m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Lae	Papua New Guinea	-6.7°	147.0°	10–30m	■	–	–	–	–	–	–	–	■	–	–	■	–	–	–	–	–
Lae Botanical Garden	Papua New Guinea	-6.721°	146.995°	10–30m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Port Moresby	Papua New Guinea	-9.48°	147.13°		■	–	–	–	–	–	–	–	■	–	–	■	■	■	–	–	–
Brown River	Papua New Guinea	-9.202°	147.235°	25–35m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Sogeri Plateau	Papua New Guinea	-9.417°	147.517°	480–520m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Kokoda	Papua New Guinea	-8.878°	147.741°	350–365m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Popondetta	Papua New Guinea	-8.758°	148.244°	75–115	–	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Wanigela	Papua New Guinea	-9.32°	149.14°	5–250m	–	–	–	–	–	–	–	–	■	–	–	–	–	–	■	–	–
Serina Beach, fruit shed	Australia	-21.380°	149.285°	35–40m	■	–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–
Rockhampton	Australia	-23.330°	150.478°	14m	–	–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–
Kavieng	Papua New Guinea	-2.57°	150.80°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corindi	Australia	-30.0161°	153.1263°	105m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mt Austen	Solomon Islands	-9.488°	159.988°	300–400m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ndondo SE1	Solomon Islands	-9.4373°	160.1156°	0–5m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Col d'Amieu 380–470m	New Caledonia	-21.0°	165.0°	380–470m	■	–	–	–	■	–	–	–	–	–	–	–	–	–	–	–	–
Col des Roussettes	New Caledonia	-21.0°	165.0°		■	–	–	–	■	–	–	–	–	–	–	–	–	–	–	–	–
Thi	New Caledonia	-22.0°	166.0°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Yaté	New Caledonia	-22.0°	166.0°		–	–	–	–	■	–	–	–	–	–	–	–	–	–	–	–	–
Noumea	New Caledonia	-22.28°	166.45°	10–100m	■	–	–	–	■	–	–	–	–	–	–	–	–	–	■	–	–
Mont Koghis 400-500m	New Caledonia	-22.18°	166.51°	400–500m	–	–	–	–	■	–	–	–	–	–	–	–	–	–	–	–	–
Mont Koghis 400-600m	New Caledonia	-22.1777°	166.5103°	400–600m	–	–	–	–	■	–	–	–	–	–	–	–	–	–	■	–	–
Wé	New Caledonia	-20.9079°	167.2571°	4–6m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Rocky Point Reserve	Australia	-29.05°	167.92°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Highlands Guesthouse	Australia	-29.03°	167.93°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mt Pitt	Australia	-29.02°	167.93°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Norfolk Island	Australia	-29.02°	167.93°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Selwyn Pine Rd top end	Australia	-29.021°	167.940°	185m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Red Road track	Australia	-29.02°	167.95°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Port Vila 6SW	Vanuatu	-17.77°	168.28°	4m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Anuda Island	Solomon Islands	-11.6120°	169.8496°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nadi	Fiji	-17.85°	177.36°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Sigatoka 1.5N	Fiji	-18.133°	177.496°	20–45m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	■	–	–
Garden Sleeping Giants	Fiji	-17.738°	177.523°		–	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–
Sigatoka 6N	Fiji	-18.095°	177.547°		–	–	–	–	–	–	–	■	–	–	–	–	–	–	■	–	–
Fiji	Fiji	-18.0°	178.0°		–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–	–
Lautoka	Fiji	-18.0°	178.0°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nakorokuva	Fiji	-18.0°	178.0°		–	–	–	–	–	–	–	–	–	–	–	–	–	–	■	–	–
Suva	Fiji	-18.0°	178.0°		■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Funafuti	Tuvalu	-8.521°	179.198°	1–6m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aopo	Samoa	-13.540°	-172.523°	240–250m	■	–	–	–	–	–	■	–	–	–	–	–	–	–	–	–	–
Apolima Island	Samoa	-13.8246°	-172.1512°	5–120m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Manono Island	Samoa	-13.8501°	-172.1102°	5–20m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Malololelei	Samoa	-13.888°	-171.771°	450–550m	■	–	–	–	–	–	–	■	–	–	■	–	–	–	■	–	–
Vailima	Samoa	-13.8659°	-171.7696°	220–350m	■	–	–	–	–	–	–	–	–	–	■	–	–	–	–	–	–
Nafanua Farm	Samoa	-13.858°	-171.764°	130–140m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apia	Samoa	-13.84°	-171.76°	5–100m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	■	–	–
Afiamalu	Samoa	-13.90°	-171.73°	350–400m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leone	American Samoa	-14.342°	-170.784°	10–20m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Taputimu Farm	American Samoa	-14.355°	-170.776°	10–20m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ili Ili	American Samoa	-14.351°	-170.750°	70–80m	■	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pago Pago	American Samoa	-14.274°	-170.691°	5–20m	■	–	–	–	–	–	–	■	–	–	–	–	–	–	–	–	■

locality	country	latitude	longitude	altitude	<i>D. ananassae</i>	<i>D. atripex</i>	<i>D. imparata</i>	<i>D. lechaisei</i>	<i>D. montieri</i>	<i>D. ochrogaster</i>	<i>D. phaeopleura</i>	<i>D. pallidosa</i>	<i>D. pandora</i> sp. nov.	<i>D. anomalata</i> sp. nov.	<i>D. schugi</i> sp. nov.	<i>pallidosa</i> -like	"papuensis"-like	<i>ananassae</i> subgroup	<i>pallidosa</i> -like Wau	<i>pallidosa</i> 3038.1	<i>ananassae</i> 3038.2
Linareva bipecc site	French Polynesia	-17.550°	-149.883°	7–10m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Three Coconut pass	French Polynesia	-17.5476°	-149.8409°	366m	■	-	-	-	■	-	-	-	-	-	-	-	-	■	-	-	-
Pao Pao riparian forest	French Polynesia	-17.500°	-149.833°	5–10m	-	-	-	-	■	-	-	-	-	-	-	-	-	-	-	-	-
Moorea	French Polynesia	-17.53°	-149.83°	1–400m	■	-	-	-	■	-	-	-	-	-	-	-	-	-	-	-	-
Gump RS 0.2W	French Polynesia	-17.4902°	-149.8285°	10–10m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Belvédère	French Polynesia	-17.5469°	-149.8266°	250–350m	■	-	-	-	■	-	-	-	-	-	-	-	-	■	-	-	-
Gump Research Station	French Polynesia	-17.4904°	-149.8264°	1–2m	■	-	-	-	■	-	-	-	-	-	-	-	-	■	-	-	-
Arue	French Polynesia	-17.517°	-149.500°	122m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Society Islands	French Polynesia	-17.6°	-149.5°		■	-	-	-	■	-	-	-	-	-	-	-	-	-	-	-	-
Tahiti	French Polynesia	-17.6°	-149.5°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mahu	French Polynesia	-23.400°	-149.450°	0–50m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Avatoru	French Polynesia	-14.94°	-147.71°		■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaituha	French Polynesia	-8.00°	-140.67°	40m	■	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mt Tekao pass 4.8NW	French Polynesia	-8.8261°	-140.2000°	437m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Aakapa 2.6E	French Polynesia	-8.8190°	-140.1053°	83m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Hakahetau 0.3SW	French Polynesia	-9.3616°	-140.1050°	36m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Hakahetau 2.5S	French Polynesia	-9.3814°	-140.0995°	250m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Taiohae 3.0N	French Polynesia	-8.8858°	-140.0971°	560m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Taiohae	French Polynesia	-8.9136°	-140.0947°	25m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Hatiheu 1.4SW	French Polynesia	-8.8377°	-140.0934°	251m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Hakahetau 3.5S	French Polynesia	-9.3884°	-140.0920°	385m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Hakahetau 2.1SE	French Polynesia	-9.3727°	-140.0901°	200m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Hakahetau 3.7S	French Polynesia	-9.3894°	-140.0901°	394m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poutemoka ridge 678m	French Polynesia	-9.3902°	-140.0834°	678m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Poutemoka ridge 698m	French Polynesia	-9.3907°	-140.0827°	698m	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Taipivai 1.5NW	French Polynesia	-8.8668°	-140.0731°	34m	■	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Pouau																					

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